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The Proventriculus of Immature Anisoptera (Odonata) With Reference to Itsuse in Taxonomy.

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THE PROVENTRICULUS OF IMMATURE ANISOPTERA (ODONATA) WITH REFERENCE TO ITS USE IN TAXONOMY

A Dissertation

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ABSTRACT

The morphology of the proventriculus of forty-one species of thirty-five genera of immature Anisoptera was investigated. It was found that in some genera the proventriculus is useful in taxonomy but among other genera there is too much uniformity.

The genera Progomphus, Gomphoides, Aphylla, Hagenius, and Dromogomphus of the Gomphidae may be recognized by the structure of their proventricular plates. Of the Aeshnidae Boyeria, Aeshna, and Basiaeschna can be characterized by their proventricular plates. Epiaeschna and Coryphaeschna have plates that are approximately alike, but differ from those of other genera studied. There is a greater difference between the plates of Anax junius and Anax amazili than among the several other genera of Aeshnidae studied. Anax junius and Anax amazili can be distinguished from other Aeshnidae by the structure of their proventricular plates.

The Macromiinae are unique among the Libellulidae studied. The genera Didymops and Macromia cannot be distinguished from each other by the structure of their armature.

The proventricular plates of the genera of Corduliinae and Libellulinae are much alike; thus, are of limited use in taxonomy.

The phylogenetic relations of the families of the Anisoptera and of the genera studied based chiefly on the structure of the proventricular armature are discussed, and phylogenetic trees of the Gomphid and

Aeshnid genera are presented. A key to the nymphs studied based on the structure of the proventricular plates is included.

No correlation was observed between the number of either spines or teeth and the size of the nymph.

HISTORICAL INTRODUCTION

Although advances have been made in the past in the study of the Odonata, very little has been done concerning the significance of the proventricular armature of the nymph in taxonomy and phylogeny of the Anisoptera.

Dufour (1852), in his paper on the anatomy and physiology of the dragonfly nymph, included very small diagrammatic figures of the proventricular armature of Libellula depressa Linnaeus and Aeshna grandis Linnaeus. Schneider (1890) figured the armature of the nymph of Aeshna sp. in his work on the alimentary canal of insects. Sadones (1896) investigated the digestive and respiratory systems of immature Odonata and included an histological study of the proventriculus of Libellula depressa Linnaeus.

The most comprehensive work dealing with the proventricular armature of the immature Anisoptera was by Ris in 1896. He figured the armature of the following nymphs: a Gomphid (either Gomphus or Onychogomphus), an Aeshnid (Aeshna sp.), a species of Cordulegaster (either C. annulatus of C. bidentatus), and Cordulia sp. He examined an unnamed species of Anax and reported the armature to be of the same type as in Aeshna. He also stated that Epophthalmia sp., Diplax sp., and Libellula sp. all have the same type armature as Cordulia. He noted that the divisions Gomphidae, Aeshnidae, Cordulegasteridae, and Libellulidae were substantiated by the structure of the armature. With this study he included a copy of the phylogenetic tree given by Calvert (1893)

and a tree of his own, based chiefly on the structure of the proventricular armature of the nymphs, in which the position of Cordulegasteridae was changed.

Tillyard (1910) described and figured the armature of Synthemis eustalacta (Burmeister). In 1917 he figured a cross section of the proventriculus of the nymph of Cordulephya pygmaea Selys and the general structure of the armature of Cordulephya pygmaea Selys, Petalura gigantea Leach, Hemigomphus heteroclitus Selys, Anax papuensis Burmeister, and Austroaeschna multipunctata Martin. He discussed the general structure, phylogenetic trends, histology and function of the proventriculus of the Odonata.

In the study of the abdomen of the Odonata by Whedon (1919), descriptions were included of the external appearance of the proventriculus, the crop, and ventriculus of undesignated species of Tramea, Libellula, Plathemis, Sympetrum, and of Anax junius (Drury). He considered briefly the general types of proventricular armature of Anax and of the Libellulines, but did not give drawings.

Fraser (1925) figured the armature of Orogomphus atkinsoni Selys and Orogomphus campioni Fraser with his discussion of the position of the Chlorogomphinae.

Calvert (1927), in his report on the Odonata collected by the Barbados-Antigua expedition, stated that the proventricular armature of Orthemis ferruginea Fabricius and that of Erythemis plebeja Burmeister resemble Ris' (1896) figure of Cordulia sp.

In a paper concerning dragonflies of the South West Cape, Africa by Barnard (1937) small figures of the armature of the following species of Anisoptera nymphs are given: Mesogomphus cognatus (Rambur), Anax imperator Leach, Presba venator Barnard, and Pseudomacromia torrida Kirby.

He also mentioned that the armature of Ceratogomphus pictus Selys is similar to that of Mesogomphus, that the armature of Macromia picta Selys is similar to that of Presba, and that the genera Crocothemis, Helothemis, and Orthetrum all show strong resemblance in type of armature, of which he briefly described that of Orthetrum.

In the reclassification of the Order Odonata by Tillyard and Fraser (1938-1940), the structure of the proventricular armature of the nymphs was mentioned as evidence to help support their ideas of the phylogenetic relations of the major groups of Odonata. Original figures of the armature of unidentified species of Austrogomphus, Aeshna, and Chlorogomphus were included.

Balfour-Browne (1944), in a paper dealing with the proventriculus of the Coleoptera and other insects, included drawings of the armature of Aeshna sp. and Sympetrum sp. He briefly discussed the number of folds between the proventricular plates.

The literature reviewed in the preceding paragraphs is limited to the proventricular armature of immature Anisoptera. However, since the armature of Anisozygoptera, the Zygoptera, and the mature Anisoptera are considered in a number of the above papers, and since the study of their armature is so closely related to the present problem, this literature will be briefly summarized in the following paragraph.

Schneider (1890) figured the armature of the nymph of Agrion sp. Ris (1896) briefly described the condition of the proventriculus of the imagoes of Gomphus sp., Aeshna sp. and figured that of Cordulegaster sp. imago. He examined the armature in both immature and mature stages of eleven species of Zygoptera and discussed the phylogeny of the group.

Calvert (1899) reported on the armature in the imagoes of six species of Zygoptera and nine species of Anisoptera, and in 1911 he described the armature of a nymph of another species. Higgins (1901) published on imagoes of one hundred species in forty-seven genera of Zygoptera, and included a brief note concerning the ontogenetic development of the nymphal armature of two Zygoptera. She presented a formula for describing the general structure of the proventricular armature of all Odonata. Marshall (1914) figured the armature of the imago of Libellula quadrimaculata Linnaeus. Tillyard (1917) illustrated the armature of five Zygopteran nymphs. In 1921 he used the armature of a nymph for evidence to support his conclusion that it belonged to the suborder Anisozygoptera, and in 1928 he described the armature of another Zygopteran nymph. In a paper by Barnard (1937) the armature of nymphs of five species of Zygoptera were figured. Tillyard and Fraser (1938-1940) figured the armature of the nymph of one species of Zygoptera, and in 1943 Fraser described the armature of the nymph of another Zygopteran. In 1944 Balfour-Browne figured these structures for the nymphs of two species of Zygoptera. In 1954 Asahina included figures of the armature of the nymph of the Anisozygopteran, Epiophlebia superstes Selys in his study of the morphology of this species.

The review of literature has shown that the types of proventricular armature have been characterized for the suborders of the Odonata, and the phylogenetic relations of the suborders as indicated by these structures have been outlined. The literature has revealed illustrations of the proventricular armature of nymphs of seventeen genera of Anisoptera of which twelve are named to species. Eleven other genera are mentioned as having armature of the type shown in the various illustrations. Most of the figures are small and inadequate in detail. Only in one instance

have differences in the armature at the species level been considered (Fraser 1925). The structure of the proventriculus has not been used to establish the phylogenetic relations among genera, nor have the changes in the proventricular armature during ontogeny of the nymph been considered.

Therefore, the purpose of this investigation is to compare the structure of the proventricular armature of immature Anisoptera in order to find out the extent these structures are useful in taxonomy and phylogeny, and to study changes in armature during ontogeny of the nymph.

MATERIALS AND METHODS

All specimens were collected in Texas, preserved in 70% to 95% alcohol, and were identified by the author unless otherwise noted. Nymphs of the Anisoptera rather that the Zygoptera were used because of the greater convenience of having larger specimens for dissection and because of the availability of identified material.

Dissections were made in alcohol under a binocular microscope with magnifications of 15 X and 45 X. The ventral part of the body was slit at one side of the median line, and the gut from the region of the esophagus through the ventriculus was lifted out leaving the nerve cord and other structures intact in order that the specimen could be used for other anatomical studies. However, a break frequently occurred between the fore- and mid-gut with the result that in such cases the fore-gut alone was removed. After the muscle layers and epithelium were dissected away leaving the cuticular intima, an opening was made on the ventral side and the food was removed. In order to see the armature, the folds of the proventriculus were spread out in a wax-lined Syracuse watch glass and anchored by minuten insect pins. Permanent mounts were considered impractical because of the form of the proventricular plates. By pinning the proventriculus on wax, the plates could be manipulated to allow study from various angles. Drawings were made with a camera lucida attached to the dissecting microscope. All measurements, which are approximate rather than absolute because of the nature of the structures measured, are recorded in millimeters.

Unless otherwise stated, descriptions and measurements are based on last instar nymphs. This stage had to be approximately determined since the life cycles of most species have not been described. Head width refers to width immediately behind the eyes. Wing case measurements refer to the length of the mesothoracic wings. In the ontogenetic studies the weakly sclerotized proventricular plates of young nymphs were usually stained with acid fuchsin and studied in glycerine on microscope slides. All proventriculi were stored in vials containing the specimens from which they were dissected. This material will be kept in the author's collection.

GENERAL STRUCTURE

The proventriculus of immature Anisoptera is the region of the stomodaeum between the crop and ventriculus or mid-gut. Externally the distinction between crop and proventriculus is evident only in the relative thickness of muscle layers. The constricted caudal end is invaginated into the ventriculus forming the stomodaeal valve. This valve appears as a collar made up of the cuticular intima of the stomodaeum, and it is easily distinguished from the thin nonchitinous epithelial wall of the ventriculus (Plate I, fig. 2). In addition to this stomodaeal valve, much more of the proventriculus may be invaginated into the ventriculus (Plate I, fig. 2). The degree of invagination varies with the quantity of food present in these divisions of the gut.

The armature consists of sclerotized areas on the longitudinal folds approximately in the middle of the proventriculus. In Petalura (Petaluridae), according to Tillyard (1917), there are eight spine-bearing folds. In all families that I have studied only four armature-bearing folds were present. These range from simple sclerotized areas on the folds with posteriorly directed spines (Plate II, fig. 1) to highly sclerotized oval or somewhat trapezoidal plates with large, toothed pyramidal projections (Plate II, fig. 2), which are highly modified in some forms (Plate II, fig. 3). The symmetry varies from radial to bilateral. The plates are located on the walls of the proventriculus in a general radial pattern, but in some species a differentiation into dorsal and ventral groups is shown either in arrangement or in size of the plates.

The Libellulidae, Cordulegasteridae, and one genus of Gomphidae have definite bilateral symmetry in which the dorsal plates differ in form from the ventral plates. Between the armed folds the cuticle may show three fairly definite folds with unarmed lightly sclerotized areas (as in some of the Aeshnidae), or it may be unsclerotized and with irregular folds. In the descriptions of the armature these folds are called intercalary folds.

The dental formula used in this study is a modification of that given by Higgins (1901). Certain minor changes and additions were made in order to indicate more clearly the characteristics of the proventriculus in the higher forms.

The letter F indicates special sclerotized areas (proventricular plates) of the lining of the proventriculus. Arabic figures following the F stand for the number of spines or teeth on each. These numbers give the range in all specimens studied, since it now seems evident that the spine number is not correlated with the instar. The term spine is used for the slender projections and the term tooth refers to the thicker and more blunt projections. Numbers followed by the letters m or p refer to the teeth located on the armature as follows:

m - ridge on median side from apex to base of plate.

p - ridge on lateral side from apex to base of plate.

If the number is not followed by a letter, it represents spines either on the general surface, at the apex, or near the base of the elevated area. The large spines are denoted by the mark (′), the medium-sized ones by (″), and the small ones by (‴). If the spines are graduated in size without a definite grouping of large, medium, and small ones, the sign used refers to the average size. However, in a generalized formula representing family characteristics, the signs (′,″,‴) may be omitted

if the size is variable within the family.

When a single fold contains two groups of spines separated by a distinct interval, this condition is indicated by placing one number above the other with a horizontal line between as in common fractions, the anterior group is represented by the numerator and the posterior group by the denominator. When the proventriculus consists of a repetition of similar folds or plates, the repeated arrangement is enclosed within parentheses with the proper coefficient before the parenthesis to indicate the number of times the repetition occurs. In bilaterally symmetrical forms the first group refers to the dorsal plates and the group following the + sign refers to the ventral plates.

Examples:

Progomphus obscurus (Rambur). 4 (F $\frac{9''' \text{ to } 23''}{2''' \text{ to } 6'''}$). There are four folds with plates bearing 9 to 23 spines each. In the posterior part of the proventriculus on each fold there are 2 to 6 minor reverse spines.

Erpetogomphus designatus Hagen. 4 (F 10" to 24"). There are four folds, each of which bears 10 to 24 spines. (Plate II, fig. 1).

Epiaeschna heros (Fabricius). 4 (F 6' to 9'). There are four folds with plates bearing 6 to 9 spines each. These spines are larger in proportion to the size of the plates than those of the two preceding species. (Plate II, fig. 2).

Plathemis lydia (Drury). 2 (F 6''' to 8" m) + 2 (F 2'). The proventriculus is bilaterally symmetrical in form. The dorsal plates have 6 to 8 teeth each. There are 2 spines on the ventral plates. (Plate II, fig. 3).

PLATE I

The Proventriculus in Position in the Alimentary Canal

Basiaeschna janata

Figure 1. General view.

Figure 2. Section of the alimentary canal with the ventriculus open to show the stomodaeal valve.

Figure 3. Part of the stomodaeum with the muscle layers and epithelium removed to show the proventricular plates and the stomodaeal valve.

A - Esophagus

B - Crop

C - Proventriculus

D - Ventriculus

E - Malpighian tubule

F - Proctodaeum

G - Proventricular plate

H - Stomodaeal valve

Scale: 2 cm. = 1 mm.

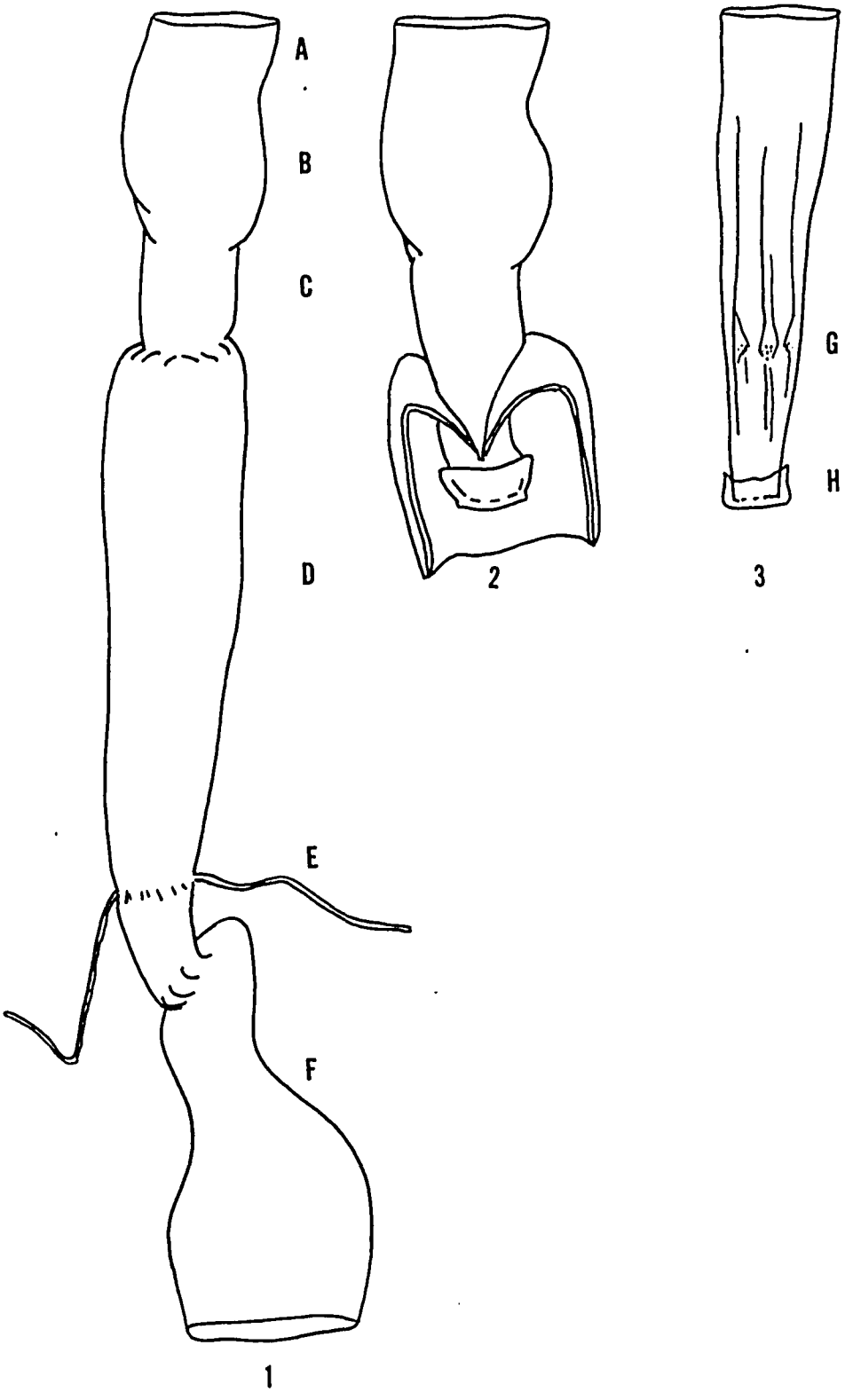

A
B
C
D
E
F
G
H
1
2
3

PLATE II

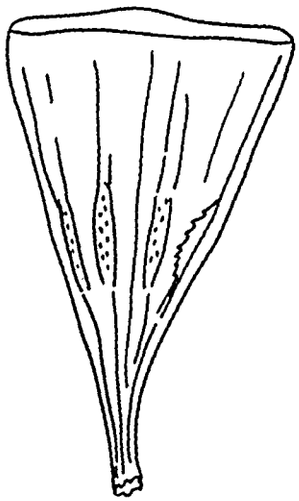
General Types of Proventriculi

Figure 1. Erpetogomphus designatus. Ventral view of proventriculus with muscle layers and epithelium removed to show bilateral symmetry.

Figure 2. Epiaeschna heros. Ventral view of proventriculus with muscle layers and epithelium removed to show radial symmetry in structure but with bilateral arrangement of plates.

Figure 3. Plathemis lydia. Ventral view of proventriculus with muscle layers and epithelium removed to show bilateral symmetry in form and arrangement.

Scale: 2 cm. = 1 mm.



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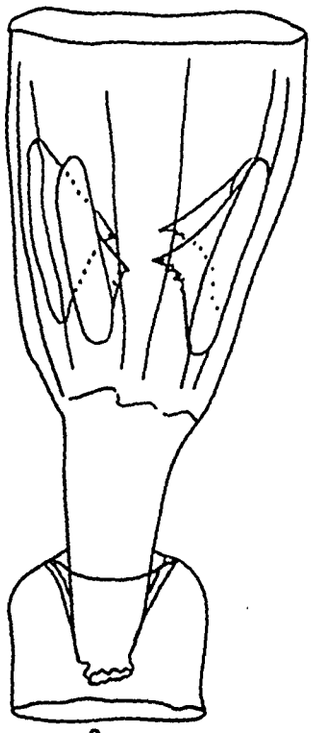

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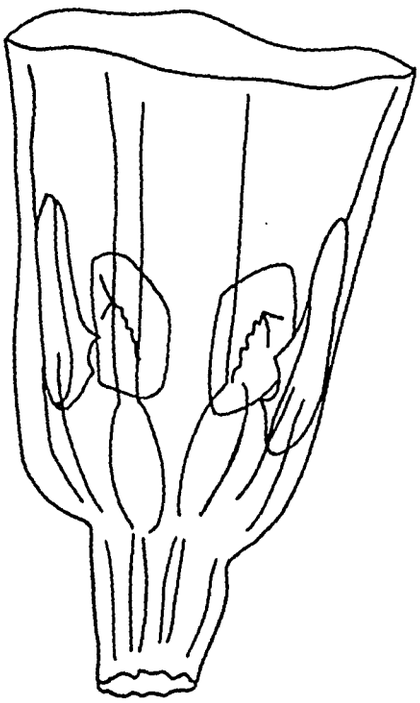


3

FAMILY GOMPHIDAE RAMBUR

GENERA AND SUBGENERA STUDIED

Progomphus Selys
Gomphoides Selys
Aphylla Selys
Gomphus Leach
  Subgenera
    Arigomphus Needham
    Gomphus Leach
    Stylurus Needham
Erpetogomphus Selys
Ophiogomphus Selys
Hagenius Selys
Dromogomphus Selys

CHARACTERISTICS OF THE GROUP

DENTAL FORMULA: 4 (F $\frac{5 \text{ to } 42}{0''' \text{to } 6'''}$).

SYMMETRY: Radial (bilateral in one genus).

SHAPE OF PLATES: Narrow, elongate; equal to or higher than the folds from which they were derived.

SIZE OF PLATES: Variable.

SPINES: Almost uniform in some species; unequal in others.

ARRANGEMENT OF SPINES: Scattered, pointed in a posterior direction; in some species grouped toward the highest area with the largest spines near the summit of the plate; in two genera, 2 to 6 minute, anteriorly pointing spines (minor reverse spines) present in the extreme posterior

region of the proventriculus on the same folds that bear the typical plates.

INTERCALARY FOLDS: Unsclerotized, irregular.

SCLEROTIZATION: Varies with the species.

DESCRIPTIONS PROVENTRICULAR ARMATURE OF SPECIES

Progomphus obscurus (Rambur)

MATERIAL STUDIED: Sixteen nymphs from Morris, Anderson, Newton, Hopkins, and Bastrop counties. Four males and five females, length 27 - 31, head width 5.5 - 5.6, wing cases 7 - 8. Three, length 19, wing cases 2; two, length 11, wing cases 0.33; two, length 7, wing cases 0.16.

DENTAL FORMULA: $4\ (F\ \frac{9''\text{ to }23''}{2'''\text{to }6'''})$.

SYMMETRY: Radial.

SHAPE OF PLATES: Width and height equal to the folds from which they were derived.

SIZE OF PLATES: Length 0.9; width 0.1.

SPINES: Almost uniform on the typical proventricular plates; minor reverse spines very small.

ARRANGEMENT OF SPINES: Scattered on the typical proventricular plates; minor reverse spines in a single row on each plate bearing fold in the extreme posterior region of the proventriculus.

SCLEROTIZATION: Weak.

SEXUAL DIMORPHISM: Not present.

VARIATION IN SPINE NUMBER: Of thirty-two plates examined, nineteen had spines ranging from 12 to 14 in number; extremes were 9 and 20.

Gomphoides stigmatus (Say)

Gomphoides albrighti Needham

MATERIAL STUDIED: Three Gomphoides stigmatus from Uvalde County; length 32 - 34, head width 6 - 6.5, wing cases 8 - 9. One Gomphoides albrighti from Comal County; length 32, head width 6, wing cases 8. No differences were observed in the proventriculi of the two species.

DENTAL FORMULA: 4 (F 17" to 27").

SYMMETRY: Radial.

SHAPE OF PLATES: Slightly wider in middle than on ends; in profile view highest at or a little posterior to the middle.

SIZE OF PLATES: Length 0.8; width 0.1.

SPINES: Graduated, with spines that are neither very large nor very small.

ARRANGEMENT OF SPINES: Scattered, but with few or no spines on sides of plates near base.

SCLEROTIZATION: Average.

Aphylla williamsoni (Gloyd)

MATERIAL STUDIED: One from East Baton Rouge Parish, Louisiana (from L.S.U. collection); length 55, head width 6, wing cases 8. Two from Broward County, Florida, collected by J. Aycock determined by G. H. Bick; length 60 - 64, head width 7, wing cases 9 - 10.

DENTAL FORMULA: $(2 + 2)$ $(F \frac{26" \text{ to } 42"}{0"' \text{ to } 4"'})$.

SYMMETRY: Bilateral.

SHAPE OF PLATES: Long, narrow, lateral and median surfaces of raised area parallel; dorsal plates highest at posterior end, ventral plates highest in the middle.

SIZE OF PLATES: Length 2.0; width 0.8.

SPINES: Graduated.

ARRANGEMENT OF SPINES: Scattered, mostly on posterior half of plates, largest on the highest area; minor reverse spines extremely small or absent in the posterior part of the proventriculus.

SCLEROTIZATION: The typical plates are well sclerotized, but the folds in the region of the minor reverse spines are not sclerotized.

Gomphus (Gomphus) descriptus Banks

MATERIAL STUDIED: One from Polk County collected by Kirk Strawn and Clark Hubbs; length 34. In the key by Needham and Westfall (1955) the nymph appears to be this species. Since some of its characteristics differ from those listed in the table accompanying the above key, this

specimen may be one of the several species of this genus whose nymphs are not yet described.

DENTAL FORMULA: 4 (F 14" to 20").

SHAPE OF PLATES: Wider than the folds from which they were derived; highest near the posterior end.

SIZE OF PLATES: Length 1.1; width 0.16.

SPINES: Graduated, but with no very large spines.

ARRANGEMENT OF SPINES: Scattered, absent in vicinity of base in the middle part of plates.

SCLEROTIZATION: Average.

Gomphus (Stylurus) sp.

MATERIAL STUDIED: One collected from Rusk County by Kirk Strawn and Clark Hubbs; length 24. Another taken in Maverick County; length 25, head width 1.3, wing cases 1.1. Immature nymphs. The Rusk County specimen keyed to G. notatus in both E. M. Walker's 1928 paper and the key in the Needham and Westfall 1955 book. The Maverick County specimen keyed to G. olivaceous or notatus in the Walker key and to G. notatus in the Needham and Westfall key. However, these specimens do not fit the figures and descriptions given by Walker (1928).

DENTAL FORMULA: 4 (F 6" to 10") for the Rusk County specimen and 4 (F 9" to 12") for the Maverick County specimen.

SHAPE OF PLATES: Narrow, a little wider than the folds from which they

were derived.

SIZE OF PLATES: Length 0.65' width 0.08.

SPINES: Almost uniform.

ARRANGEMENT OF SPINES: Scattered.

SCLEROTIZATION: Weak.

Gomphus (Arigomphus) lentulus Needham

Gomphus (Arigomphus) maxwelli Ferguson

MATERIAL STUDIED: Two Gomphus lentulus from Hopkins and Hunt counties; length 33 and 35. One Gomphus maxwelli from Lavaca County (determined by J. G. Needham in 1951); length 27, wing cases 7.

DENTAL FORMULA: 4 (F 12" to 17") for G. lentulus and 4 (F 10" to 14") for G. maxwelli.

SYMMETRY: Radial.

SHAPE OF PLATES: Width and height equal to folds from which they were derived.

SIZE OF PLATES: G. lentulus, length 1.0; width 0.09. G. maxwelli, length 0.75, width 0.05.

SPINES: Almost uniform.

ARRANGEMENT OF SPINES: Scattered.

SCLEROTIZATION: Weak.

Erpetogomphus designatus Hagen

MATERIAL STUDIED: Fourteen (six males and eight females) from Bexar, Burnet, Fayette, and Travis counties. Twelve, length 22 - 24, head width (of two males) 5, wing cases 6 - 7. One, length 20, wing cases 2. One, length 17, wing cases 3.

DENTAL FORMULA: 4 (F 10" to 24").

SYMMETRY: Radial.

SHAPE OF PLATES: Slightly wider and higher than basic folds; angle at posterior end a little sharper than at anterior end.

SIZE OF PLATES: Length 0.7; width 0.1.

SPINES: Graduated.

ARRANGEMENT OF SPINES: Scattered, with the smaller spines at the ends.

SCLEROTIZATION: Average.

SEXUAL DIMORPHISM: Not present.

VARIATION IN SPINE NUMBER: Of the fifty-six plates examined, thirty-five had from 13 to 17 spines each; extremes were 10 and 24.

Ophiogomphus colubrinus Selys

MATERIAL STUDIED: One from Cheboygan County, Michigan, collected by G. H. Bick and identified by E. M. Walker in 1950.

DENTAL FORMULA: 4 (F 12" to 16").

SYMMETRY: Radial.

SHAPE OF PLATES: Wider than basic folds; slightly higher in the middle.

SIZE OF PLATES: Length 0.7; width 0.1.

SPINES: Differentiated into small and medium size spines.

ARRANGEMENT OF SPINES: Scattered.

SCLEROTIZATION: Average.

Hagenius brevistylus Selys

MATERIAL STUDIED: Seven from Bandera, Real, and Hardin counties, and one from Tangipahoa Parish, Louisiana, collected by R. D. Suttkus. Three, length 40 - 42, head width 7, wing cases 10 - 11; one, length 31, head width 7, wing cases 5; one, length 26, wing cases 3; three, length 14, head width 2.5, wing cases 0.5.

DENTAL FORMULA: 4 (F 5" to 13").

SYMMETRY: Radial.

SHAPE OF PLATES: Wider in middle than at ends; in profile view, highest in or immediately posterior to middle.

SIZE OF PLATES: Length 0.6 - 0.7; width 0.15.

SPINES: Almost uniform.

ARRANGEMENT OF SPINES: Scattered.

SCLEROTIZATION: Average.

VARIATION IN SPINE NUMBER: Of thirty-two plates examined, twenty-three had from 7 to 10 spines; extremes were 5 and 13.

Dromogomphus spoliatus Hagen

Dromogomphus spinosus Selys

MATERIAL STUDIED: Four D. spoliatus from Bastrop (collected by Kirk Strawn and Clark Hubbs), Kimble, and Hunt counties. One, length 33, head width 5; three, length 31, head width 4.5 - 5.5, wing cases 7 - 8. Two D. spinosus collected by Kirk Strawn from Menard and Tyler counties; length 28-32, head width 6 (of the larger specimen), wing cases 9 (of the larger specimen).

DENTAL FORMULA: D. spoliatus, 4 (F 27" to 41"). D. spinosus, 4 (F 28" to 32").

SHAPE OF PLATES: Elevated area with rounded sides, not parallel as in Aphylla.

SIZE OF PLATES: D. spoliatus, length 1.6, width 0.17. D. spinosus, length 1.2; width 0.16.

SPINES: Graduated; extremes, very large and very small.

ARRANGEMENT OF SPINES: Largest on highest area.

SCLEROTIZATION: Well sclerotized.

TABLE I

Comparison of the Proventricular Plates of

D. spinosus with *D. spoliatus*

Structure	*D. spinosus*	*D. spoliatus*
Length of plates compared to length of body	Shorter, 1.2/32	Longer, 1.6/31
Highest point as seen from profile view.	Slightly posterior to middle.	At middle.
Posterior end compared with anterior end.	Anterior end less inclined than posterior end.	Anterior and posterior inclined to equal degree.
Size of largest spines.	Smaller, 0.06	Larger, 0.09
Distribution of spines toward ends of plates.	More scattered at ends.	Closer together at ends.
Size of spines on sides of plates.	Smaller.	Larger.

WORK OF OTHER INVESTIGATORS

GENERA AND SPECIES STUDIED:

Gomphus or Onychogomphus - Ris 1896. One plate with twenty-four spines. There are probably ten additional spines on the side not shown. The spines appear to be slightly larger than those of such forms as Gomphus, Erpetogomphus, and Ophiogomphus which have the relatively undifferentiated plates as shown in Ris' figure.

Hemigomphus heteroclitus Selys - Tillyard 1917. Very small figures of two plates showing twenty and twenty-one spines.

Mesogomphus cognatus (Rambur) - Barnard 1937. Small diagrammatic figure of one plate with seventeen spines.

Ceratogomphus pictus Selys - Barnard 1937. No figure given, but Barnard mentioned that the armature of this species is similar to that of Mesogomphus.

Austrogomphus sp. - Tillyard and Fraser 1938 - 1940. Diagrammatic figure of one plate showing nineteen spines.

SIGNIFICANCE:

Since the size of the nymphs, the size of the plates, and other details are not given for the above forms, it is impractical to compare the above genera with those which I have studied.

ONTOGENETIC STUDIES

SPECIES STUDIED:

Progomphus obscurus (Rambur). Spines per typical proventricular plate range in number from 10 to 16 in the seven and eleven millimeter nymphs; in the nineteen millimeter nymphs from 9 to 23; and in the twenty-seven to thirty-one millimeter nymphs from 9 to 20.

Erpetogomphus designatus Hagen. Spines per plate range in number from 10 to 17 in the seventeen and twenty millimeter nymphs, which is within the limits of variation (10 - 24) shown by the twenty-four millimeter nymphs.

Hagenius brevistylus Selys. Spines per plate range in number from 7 to 13 in the fourteen millimeter nymphs; from 9 to 13 in the twenty-six millimeter nymph; from 7 to 10 in the thirty-one millimeter nymph; and from 5 to 13 in the forty to forty-two millimeter nymphs.

SIGNIFICANCE:

There does not appear to be a correlation between size and the number of spines in the immature Gomphines.

TABLE II

Diagnostic Characteristics of

Genera and Subgenera of the Gomphidae

Genus	Spines	Characteristics
Progomphus	9" - 23" / 2"'-6"'	Minor reverse spines; simple narrow plates.
Aphylla	26"- 43" / 0"'- 4"'	Bilateral symmetry
Hagenius	5" - 13"	Wide, short plates; relatively few spines.
Dromogomphus	27"- 41"	Long plates with very large spines on high middle area.
Gomphoides	17"- 27"	Spines small, graduated in size; concentrated to a degree toward summit of plate.
Erpetogomphus*	10"- 24"	Length equals six times width; posterior end not higher than anterior end.
Ophiogomphus*	12"- 16"	Length equals six times width; much like Erpetogomphus.
Gomphus (Arigomphus)*	10"- 17"	Simple, narrow plates; length equals ten times width.
Gomphus (Stylurus)*	6" - 10"	Few spines, narrow plates; length equals eight times width.
Gomphus (Gomphus)*	14"- 20"	Posterior end higher than anterior end; length equals six times width.

* Genera that are very difficult to distinguish.

PHYLOGENY

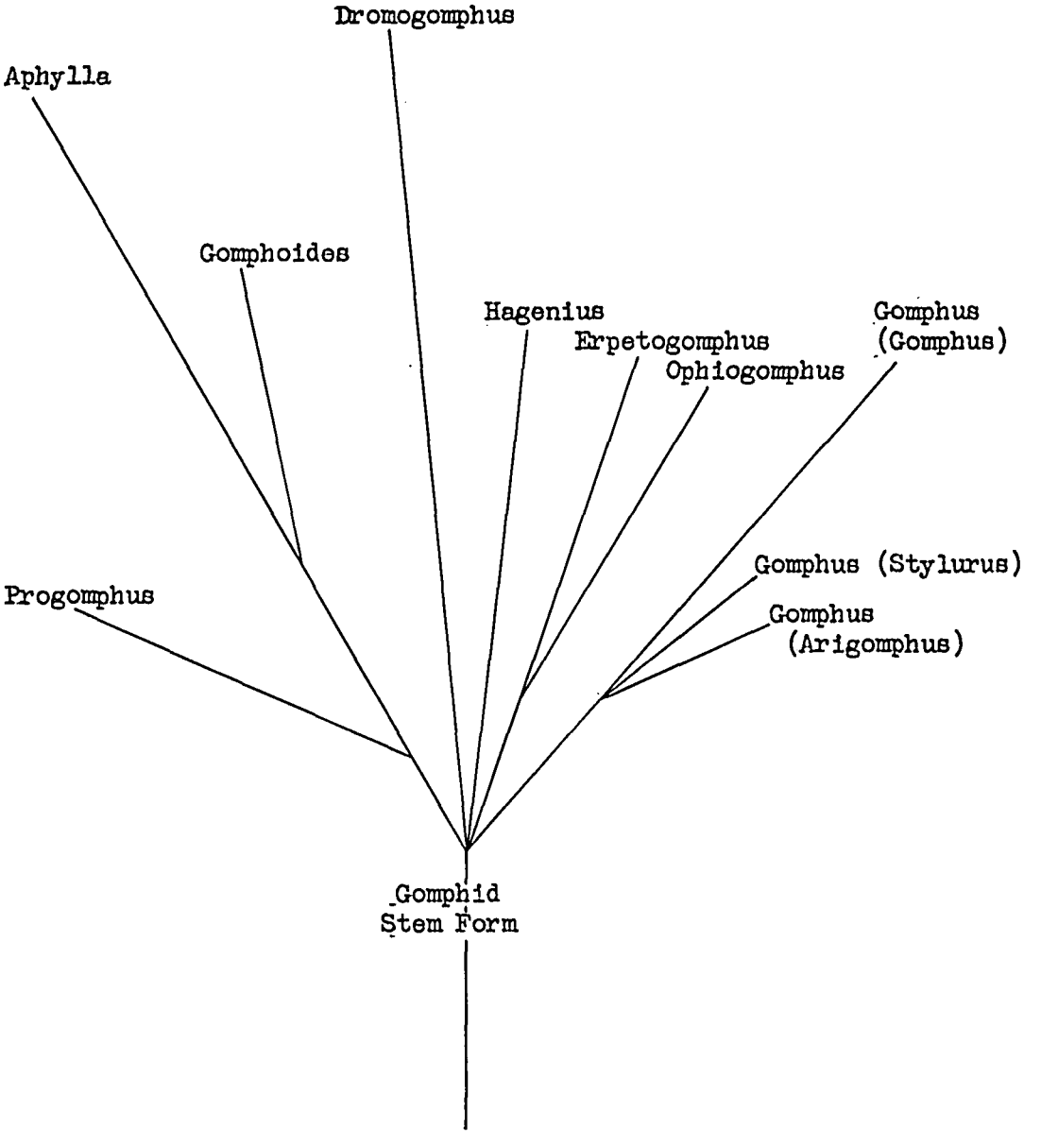


Figure 1. Phylogenetic relations of the genera of the Gomphidae

TABLE III

Degrees of Specialization of

Genera and Subgenera of the Gomphidae

Genus	Characteristics and Degree of Specialization*									
	I	II	III	IV	V	VI	VI	VIII	IX	Total**
Progomphus	1	2	1	1	1	1	1	1	2	11
Gomphoides	2	1	1	2 b 2 c	2	2	2	1	2	15
Aphylla	1	3	2 a	2 c 2 b	2 1	3	3	2	3	21
Gomphus (Arigomphus)	1	1	1	1	1	1	1	1	2	10
Gomphus (Stylurus)	2	1	1	1	1	1	1	1	1	10
Gomphus (Gomphus)	2	1	1	2 c	2	3	2	1	2	16
Erpetogomphus	2	1	1	2 a	2	1	1	1	2	13
Ophiogomphus	2	1	1	2 a	1	2	1	1	2	13
Dromogomphus	2	1	2 a	2 b	1 2	4	3	1	3	20
Hagenius	3	1	2 b	2 c	2	1	1	1	1	13

* See list of characteristics and degrees of specialization.

** Total number represents the degree of specialization and is used in accompanying phylogenetic chart.

PHYLOGENY

The relationships among the genera of the Gomphidae based on the structure of the proventricular armature are shown in the phylogenetic tree. The distance between the Gomphid stem form and the genus on the chart represents the degree of specialization of the genus. The positions on the tree indicate the relations of the genera.

The degrees of specialization are shown on the chart, and were derived by a comparison of the morphology of the proventricular plates as given in the outline which follows the chart. The Roman numerals refer to the general types of characteristics and the Arabic numbers represent the degree of specialization. If two or three variations listed under a general character are of equal degree of specialization, this is indicated by the same specialization number. In the outline the number is subdivided by a, b, etc.

SPECIALIZATION KEY

I. Width of plates.

1. Very narrow, approximately equal to the basic folds.
2. Wider than basic folds, margins almost parallel.
3. Wider than basic folds, slightly wider in middle than at end.

II. Minor reverse spines.

1. Absent.
2. Present, well developed.
3. Present, but very degenerate in size.

III. Length of plates.

1. Of average length (long).

2. a) Extra long.

2. b) Reduced in length.

IV. Height of plates.

1. Same as of basic folds.

2. a) Higher than basic folds, almost the same throughout.

2. b) Higher than basic folds, highest in middle.

2. c) Higher than basic folds, highest at posterior end.

V. Anterior and posterior ends, profile view.

1. Both gradually inclined toward base.

2. Posterior end with a sharper incline.

VI. Size of spines.

1. Approximately equal.

2. Graduated, largest spines of small size.

3. Graduated, largest spines of medium size.

4. Graduated, with very large spines.

VII. Arrangement of spines.

1. Scattered.

2. Scattered, but absent on sides very near base.

3. a) Scattered, but absent on sides of anterior half of plates, with larger spines on highest area.

3. b) Scattered, with very large spines on highest area.

VIII. Symmetry.

1. Radial.

2. Bilateral.

IX. Number of spines.

1. Five to thirteen.

2. Nine to twenty-seven.

3. Twenty-six to forty-three.

DISCUSSION

The Gomphid stem form probably had four, lightly sclerotized, narrow proventricular plates with small, scattered spines. Early in the ancestry of the group a branch evidently originated with minor reverse spines. (This is discussed further in the section on general phylogenetic considerations.) Progomphus is the most primitive of this group, and Aphylla is the most highly specialized. Since the typical proventricular plates of these two genera are very diverse in form, the only reason, according to the morphology of the proventriculus, to associate the two genera is the presence of the minor reverse spines. In Aphylla they are so small that it is difficult to find them. The genus Gomphoides has plates that may be considered as intermediate between the above two. I could not, however, find any vestiges of minor reverse spines.

Selys (1858) placed Progomphus, Hagenius, and Gomphoides in his Legion II of the Division Integrilabiees with Gomphoides and Aphylla as subgenera of Gomphoides. Williamson (1920) separates this division into six series in which he elevates Hagenius to the level which parallels his Progomphus series. My study supports this separation of Hagenius but does not corroborate the opinion that Aphylla is a subgenus of Gomphoides.

Tillyard and Fraser (1938-1940) place Dromogomphus in the subfamily with Erpetogomphus, Ophiogomphus, and Gomphus (sensu latu). My work does not indicate that Dromogomphus is closely related to these

genera, although it does show that Ophiogomphus, Erpetogomphus, and Gomphus (sensu latu) have proventricular plates of the same type. Both Hagenius and Dromogomphus, according to their proventricular plates, show no special affinities toward the other genera studied.

PLATE III

Progomphus obscurus

Ventral view of open proventriculus showing the typical proventricular plates and the minor reverse spines.

Scale: 2 cm. = 0.33 mm.

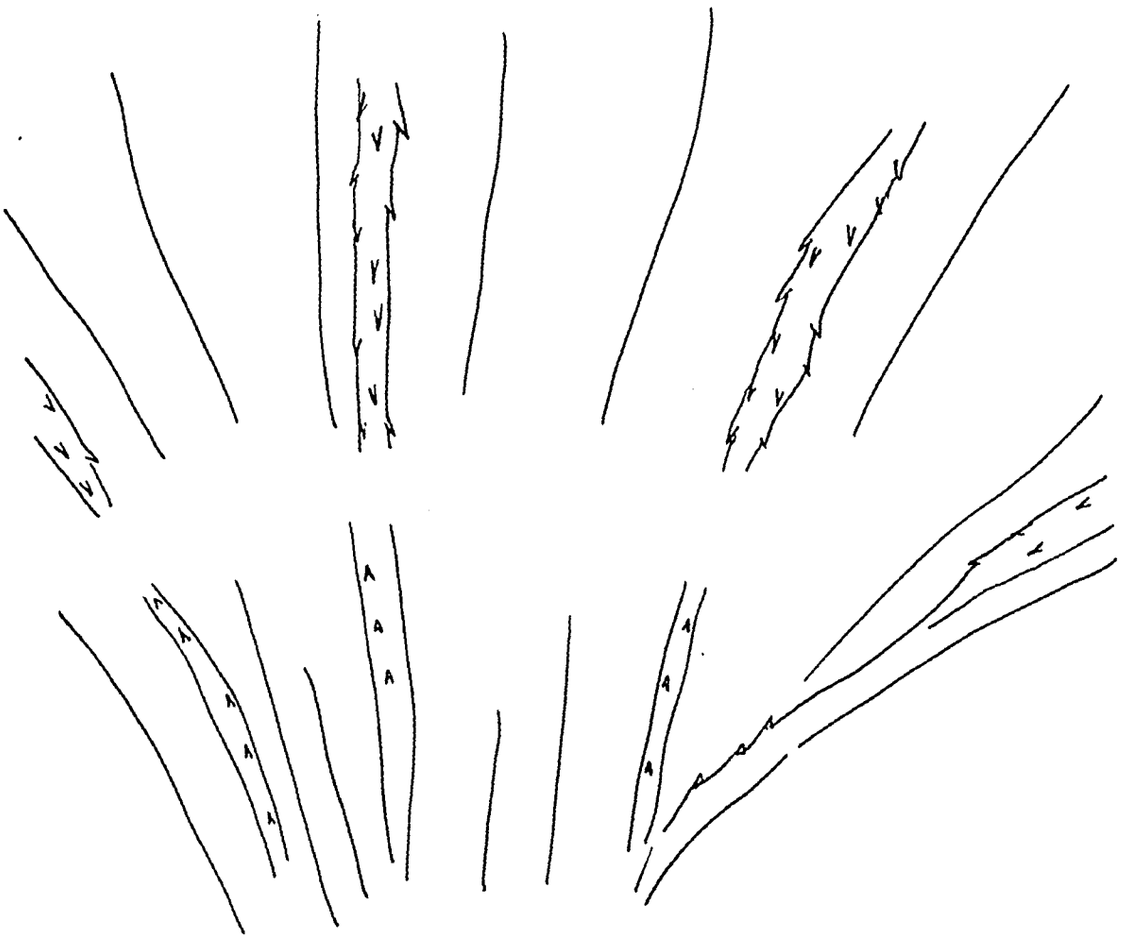


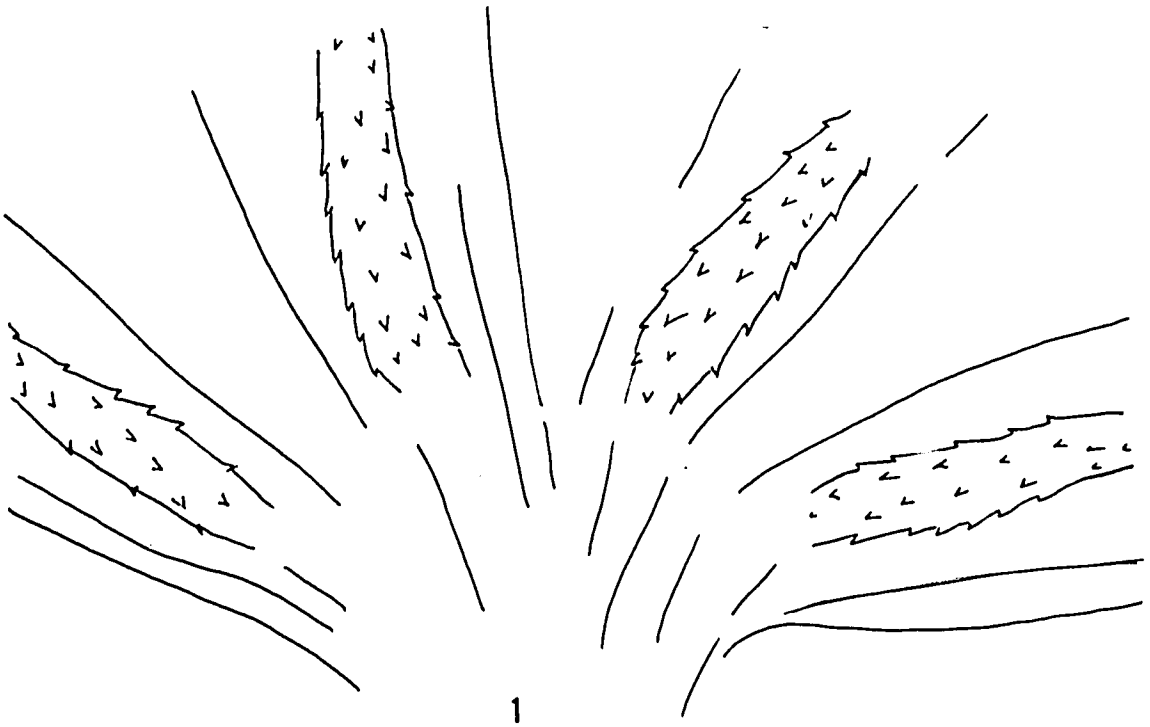
PLATE IV

Gomphoides stigmata

Figure 1. Ventral view of open proventriculus showing the proventricular plates.

Figure 2. Lateral view of the proventricular plates.

Scale: 2 cm. = 0.33 mm.



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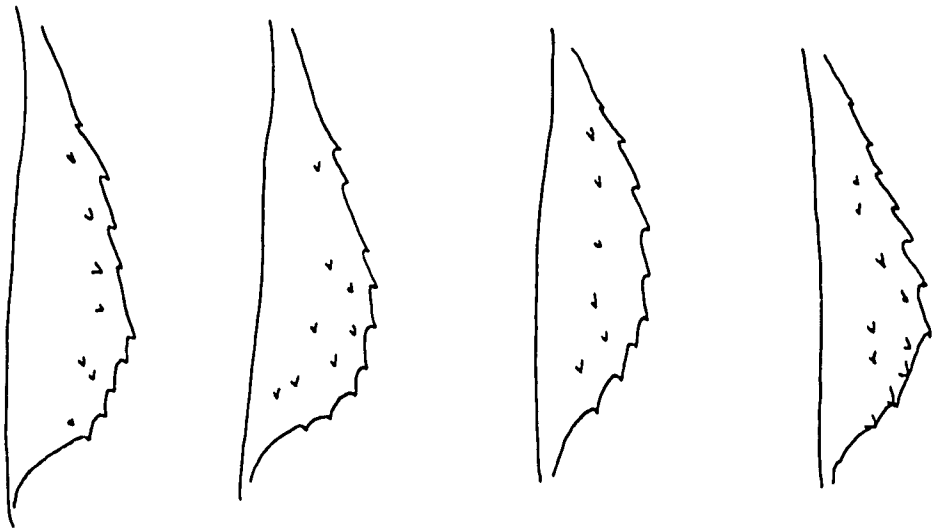


2

PLATE V

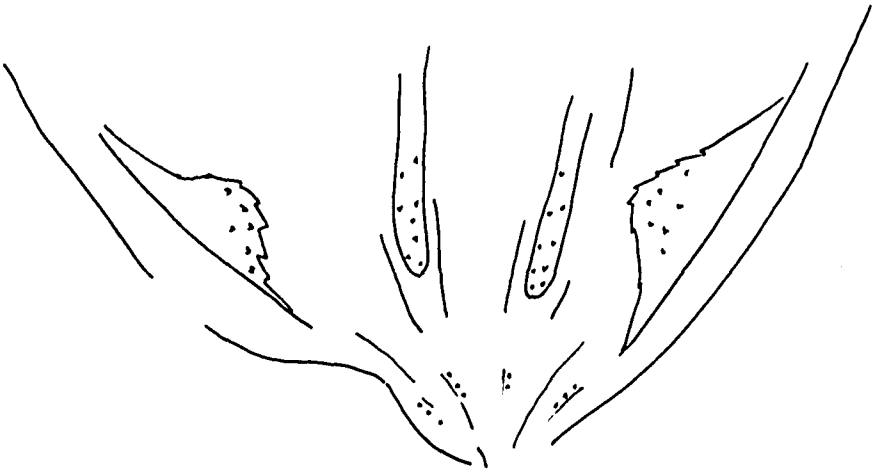
Aphylla williamsoni

Figure 1. Ventral view of the open proventriculus showing the typical proventricular plates and the minor reverse spines.

Scale: 2 cm. = 1 mm.

Figure 2. Lateral view of the typical proventricular plates.

Scale: 2 cm. = 0.33 mm.



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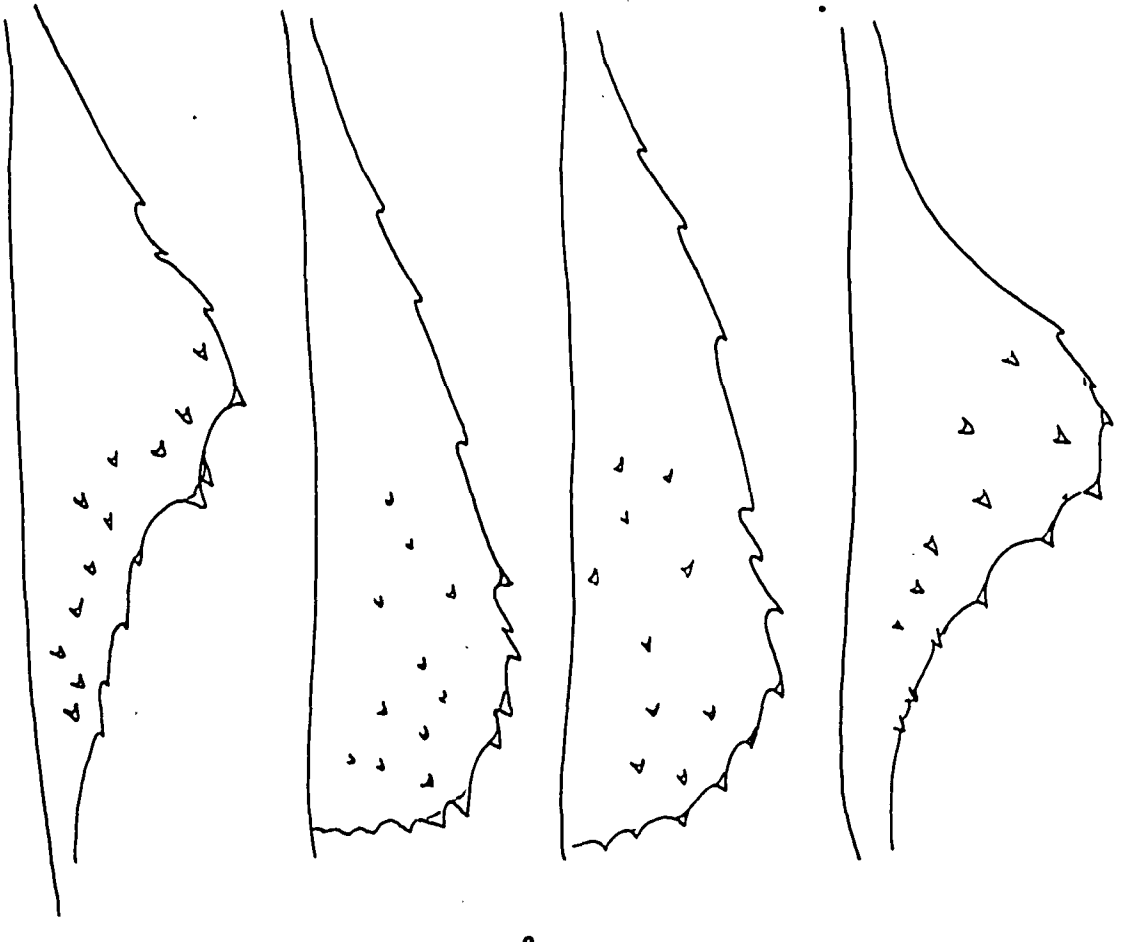


2

PLATE VI

Aphylla williamsoni

Figure 1. Fold showing a ventral proventricular plate and minor reverse spines.

Figure 2. Fold showing a dorsal proventricular plate and minor reverse spines.

Scale: 2 cm. = 0.33 mm.

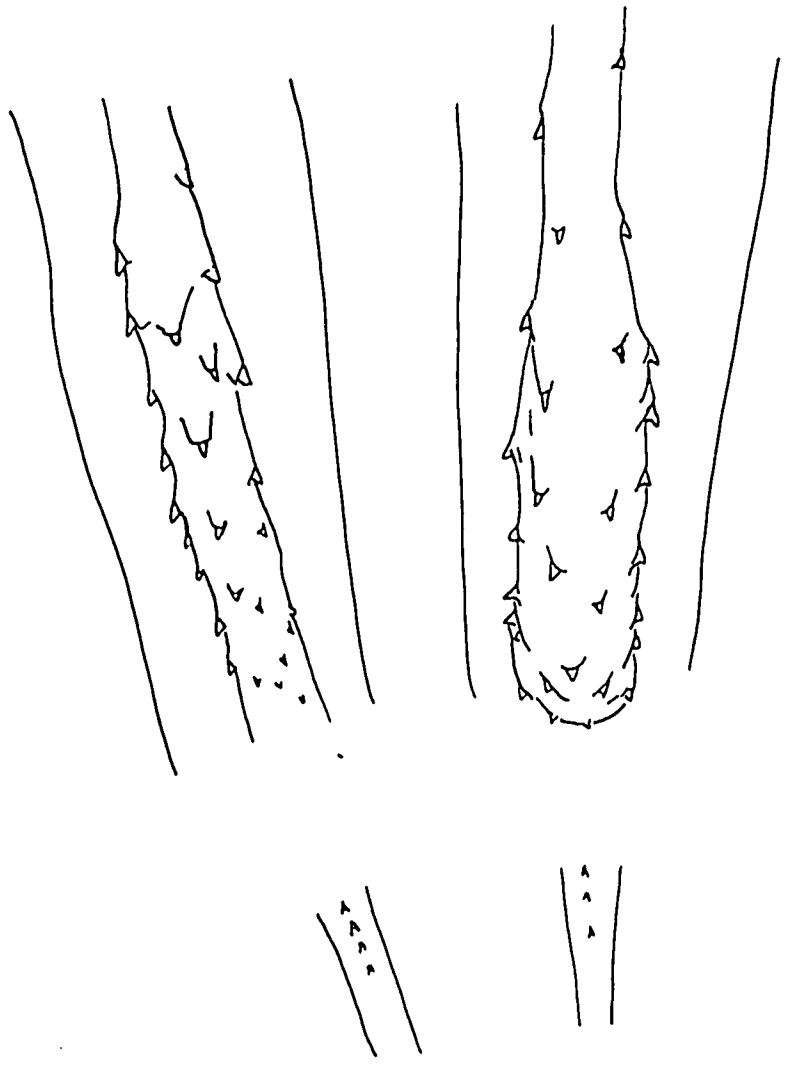

1
2

PLATE VII

Gomphus (*Gomphus*) *descriptus*

Ventral view of open proventriculus showing the proventricular plates.

Scale: 2 cm. = 0.33 mm.

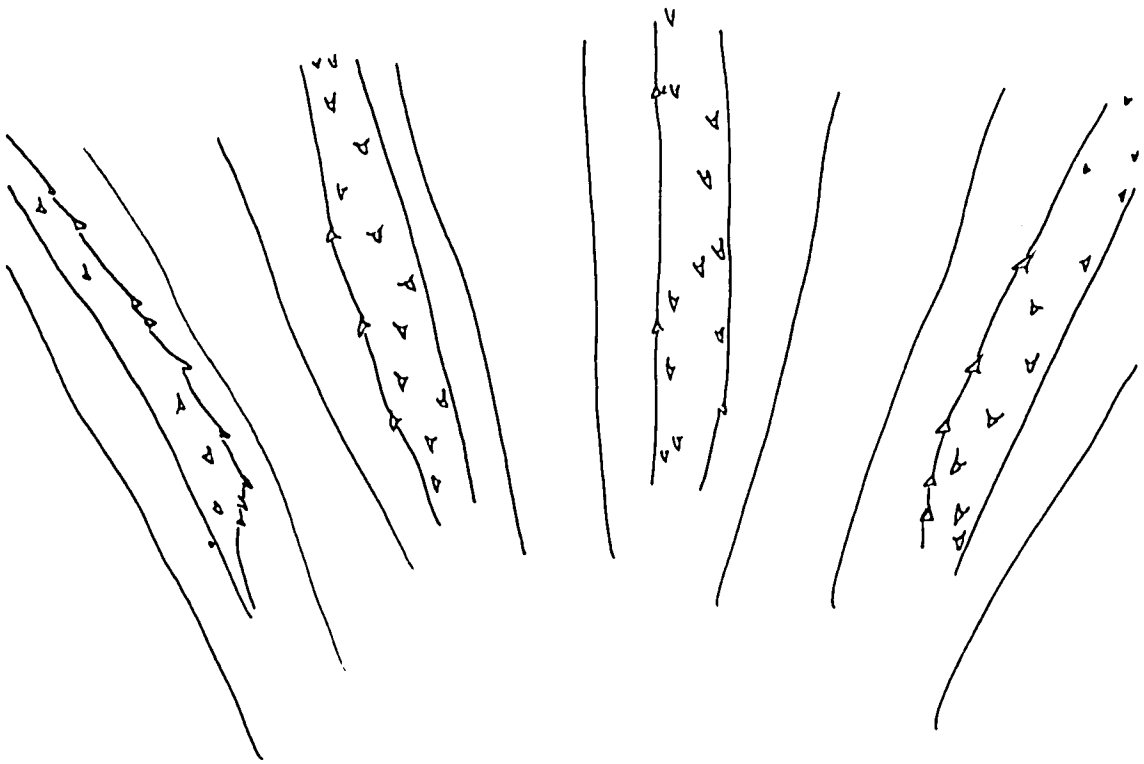


PLATE VIII

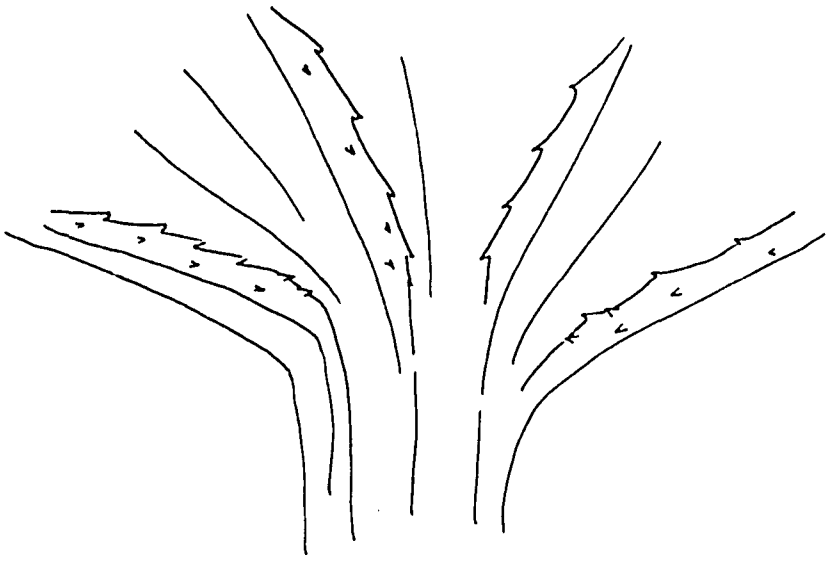
Gomphus (*Stylurus*) sp., *Gomphus* (*Arigomphus*) *lentulus*, and *Gomphus* (*Arigomphus*) *maxwelli*

Figure 1. Ventral view of open proventriculus of *Gomphus* (*Stylurus*) sp. showing proventricular plates.

Figure 2. Proventricular plate of *Gomphus* (*Arigomphus*) *lentulus*.

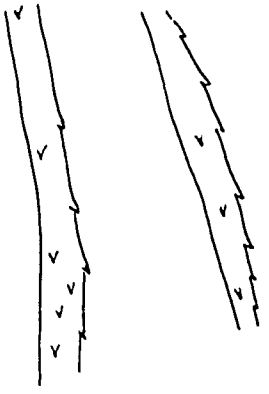
Figure 3. Two proventricular plates of *Gomphus* (*Arigomphus*) *maxwelli*.

Scale: 2 cm. = 0.33 mm.



1

2



3

PLATE IX

Erpetogomphus designatus

Ventral view of open proventriculus showing proventricular plates.

Scale: 2 cm. = 0.33 mm.

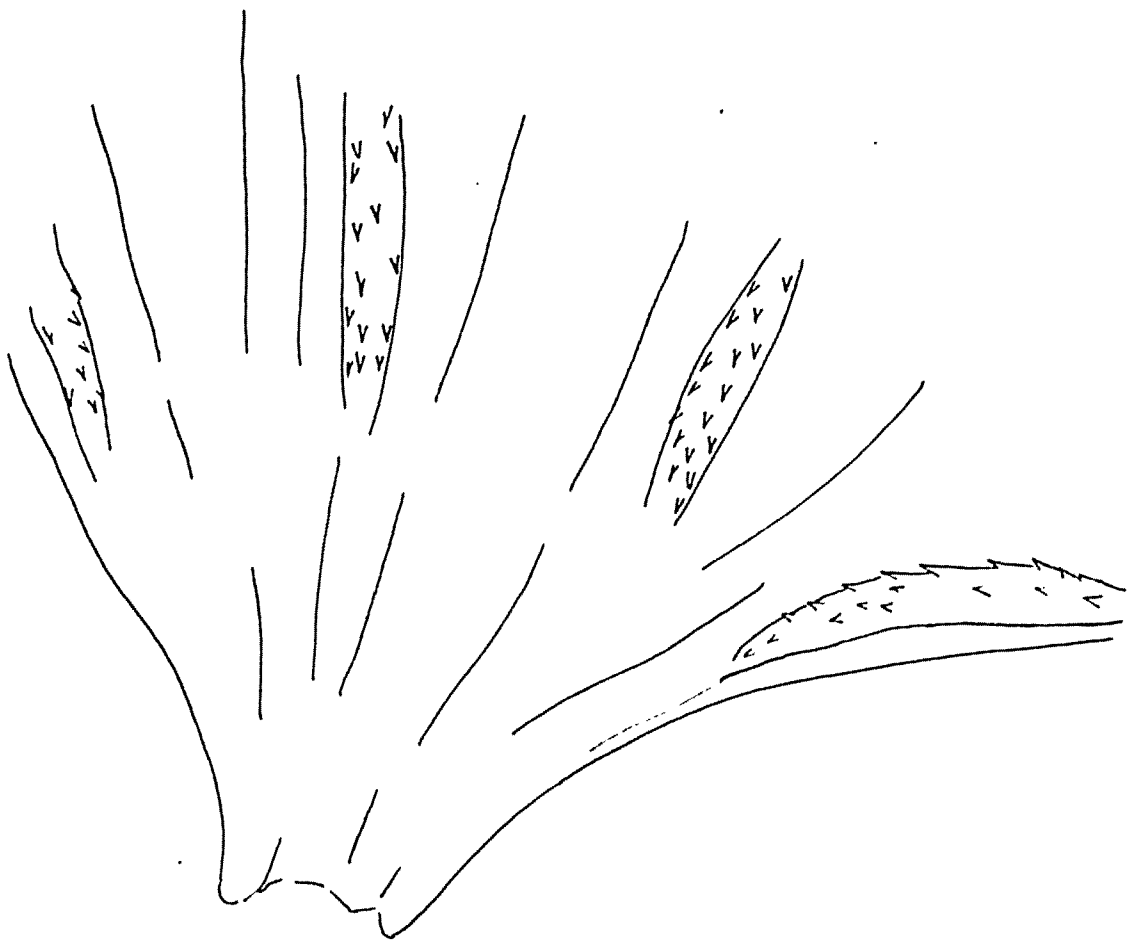


PLATE X

Ophiogomphus colubrinus

Ventral view of open proventriculus showing proventricular plates.

Scale: 2 cm. = 0.33 mm.

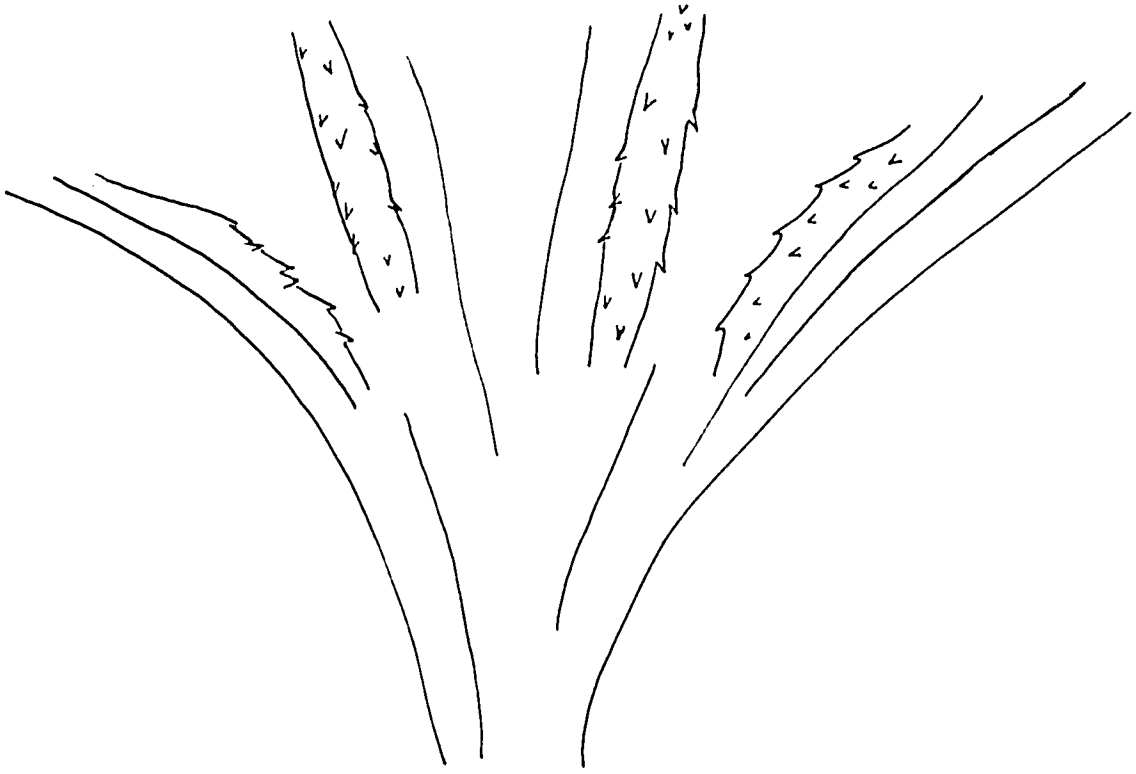


PLATE XI

Hagenius brevistylus

Ventral view of open proventriculus showing proventricular plates.

Scale: 2 cm. = 0.33 mm.

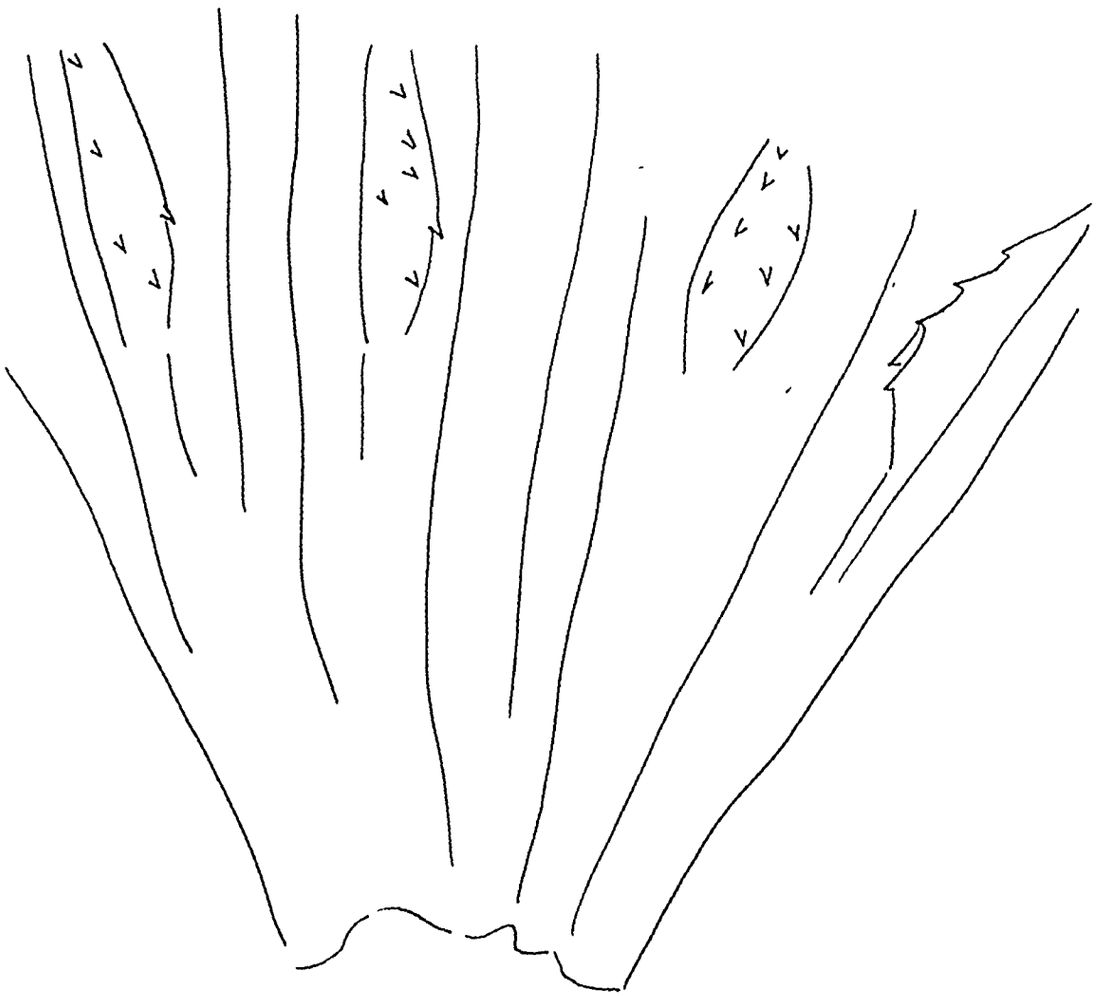


PLATE XII

Dromogomphus spoliatus

Ventral view of proventricular plates.

Scale: 2 cm. = 0.33 mm.

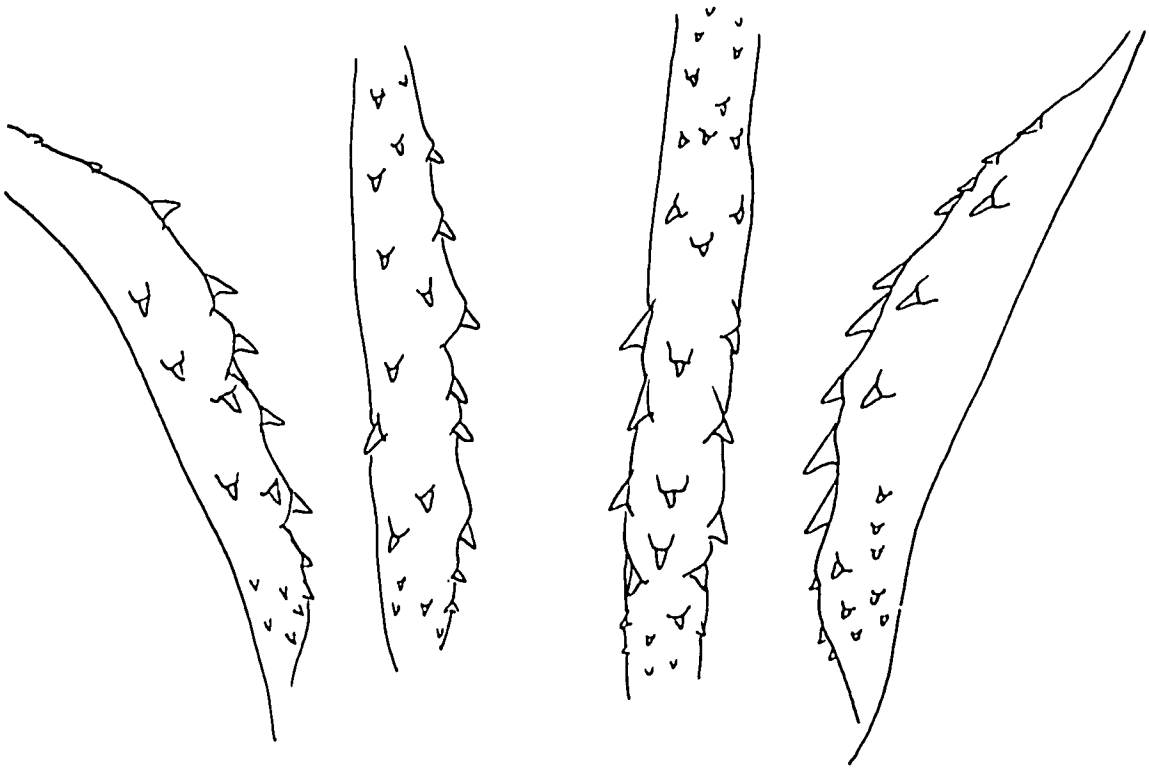


PLATE XIII

Dromogomphus spoliatus

Ventral view of proventricular plates. Compare with Plate XII to note variation in size of spines.

Scale: 2 cm. = 0.33 mm.

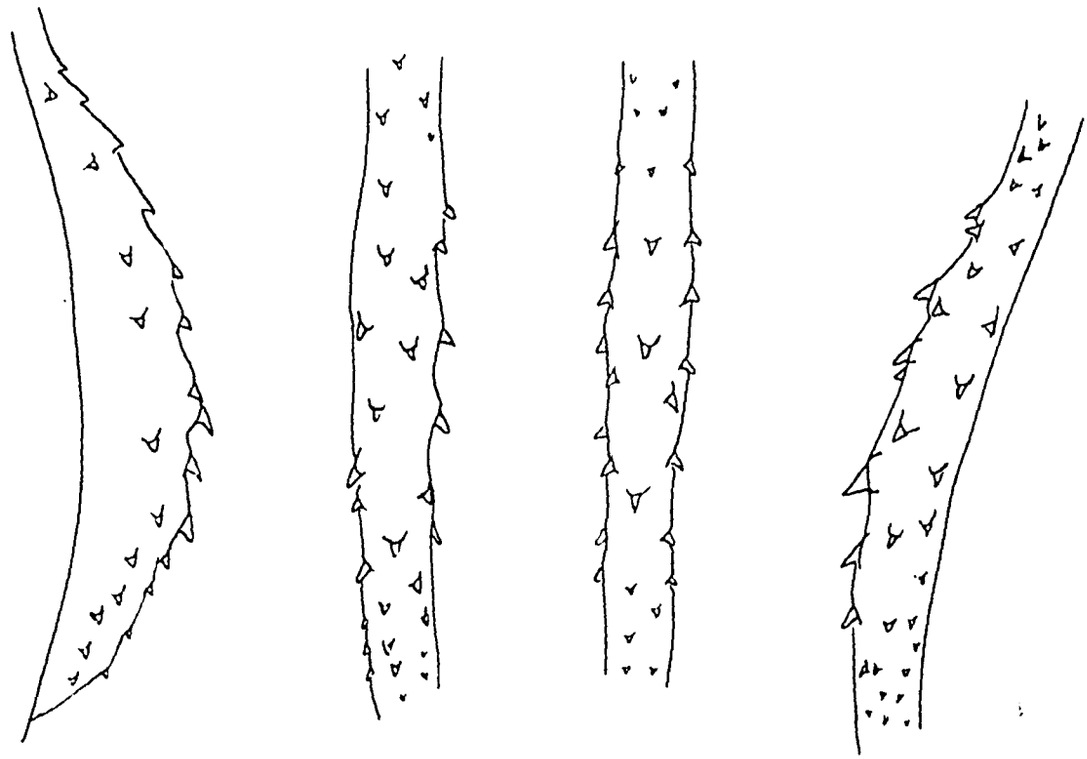
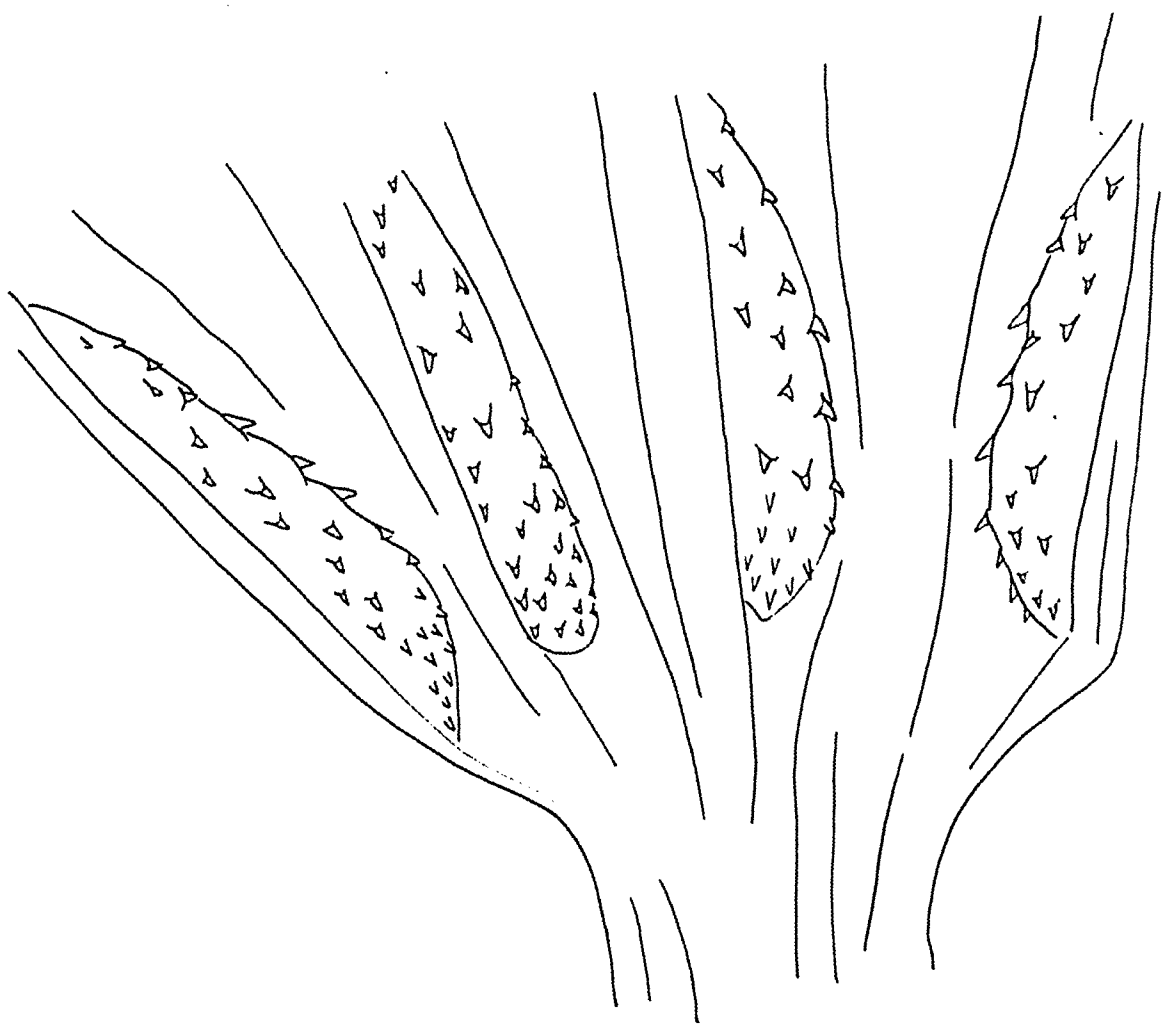


PLATE XIV

Dromogomphus spinosus

Ventral view of open proventriculus showing proventricular plates.

Scale: 2 cm. = 0.33 mm.



FAMILY AESHNIDAE SELYS

GENERA STUDIED

Aeshna Fabricius
Boyeria MacLachlan
Anax Leach
Coryphaeschna Williamson
Nasiaeschna Selys
Basiaeschna Selys
Epiaeschna Hagen

CHARACTERISTICS OF THE GROUP

DENTAL FORMULA: 4 (F 2 to 20).

SYMMETRY: Radial (Arrangement slightly bilateral, the dorsal plates are a little anterior to the ventral plates).

SHAPE OF PLATES: Spines on a somewhat elevated area which has an oval base on a flat, lightly sclerotized section of the wide fold; herein this elevated area is considered the proventricular plate. There is almost no variation in the shape of the base.

SIZE OF PLATES: Variable.

SPINES: Almost uniform in some species; unequal in others.

ARRANGEMENT OF SPINES: Clustered near the apex in different patterns; no minor reverse spines.

INTERCALARY FOLDS: Three, of different widths, between the folds with plates; lightly sclerotized as are the flat areas that bear the plates.

SCLEROTIZATION: Elevated areas well sclerotized; flat bases and intercalary folds variable.

DESCRIPTIONS PROVENTRICULAR ARMATURE OF SPECIES

Aeshna umbrosa Walker

MATERIAL STUDIED: One collected by Ottys and Ruth Sanders near Hot Springs, Arkansas; length 31, head width 7, wing cases 4.5; probably not a last instar nymph, since according to Needham and Westfall (1955) the length should be from 38 to 44.

DENTAL FORMULA: 4 (F 6' to 7').

SHAPE OF PLATES: Apex about two-thirds distance from the anterior to posterior end; in profile view, apical angle equals about 100°.

SIZE OF PLATES: Length 0.8; width 0.2.

SPINES: Almost uniform.

ARRANGEMENT OF SPINES: From apex to base on either side and slightly posterior in position.

INTERCALARY FOLDS: Middle fold a little wider than the lateral folds.

SCLEROTIZATION: Bases and intercalary folds lightly sclerotized; plates average.

Boyeria vinosa (Say)

MATERIAL STUDIED: Five from Harrison (Kirk Strawn and Clark Hubbs,

collectors), Livingston (Ruth Sanders, collector), Hardin, and Titus counties. One, length 29, head width 4.7, wing cases 4 - 4.7; two, length 13 - 15, head width 2.5. wing cases 0.5.

DENTAL FORMULA: 4 (F 3' to 5').

SHAPE OF PLATES: Apex about two-thirds distance from anterior to posterior end; in profile view, apical angle equals about 100°.

SIZE OF PLATES: Length 0.54, width 0.16.

SPINES: Graduated.

ARRANGEMENT OF SPINES: From apex to base on either side in a row, the lower spines are slightly anterior to the apical spine.

INTERCALARY FOLDS: Middle fold wider than lateral folds.

SCLEROTIZATION: Plates average; bases and intercalary folds not sclerotized.

VARIATION IN SPINE NUMBER: Of sixteen plates tabulated, one had 3, seven had 4, and eight had 5 spines.

ONTOGENETIC STUDIES: The thirteen and fifteen millimeter nymphs had plates similar to those of the twenty-nine millimeter nymphs.

Anax junius (Drury)

MATERIAL STUDIED: Five from Aransas and Dallas counties; length 43, head width 8 - 10, hind wings 11.

DENTAL FORMULA: 4 (F 2" to 3" + 11"' to 23"').

SHAPE OF PLATES: Apex approximately two-thirds distance from anterior to posterior end; apical angle in profile view equals 90° to 105°.

SIZE OF PLATES: Length 1.0, width 0.33.

SPINES: The two or three apical spines are larger than those on the sides.

ARRANGEMENT OF SPINES: Small spines show a tendency to be concentrated in a row from apex to base on either side of apex.

INTERCALARY FOLDS: Almost equal in width.

SCLEROTIZATION: Intercalary folds and flat bases lightly sclerotized; plates average.

Anax amazili (Burmeister)

MATERIAL STUDIED: Four from Hays and Uvalde counties, and one taken by Ruth and Ottys Sanders from Tamazunchale, Mexico. The Mexican specimen had length of 19, head width 4.5, wing cases 0.66. The Texas specimens, length 44, head width 9 - 10, wing cases 12.

DENTAL FORMULA: 4 (F 10' to 15').

SHAPE OF PLATES: Apex approximately three-fourths distance from anterior to posterior ends; apical angle in profile view equals about 55° in the large specimens, but in the 19 mm. nymph the angle is much greater (90° to 100°).

SIZE OF PLATES: Length 1.3, width 0.33.

SPINES: Graduated, fairly large.

ARRANGEMENT OF SPINES: Largest spines at and near apex.

INTERCALARY FOLDS: Middle fold wider than lateral folds.

SCLEROTIZATION: Intercalary folds and flat bases lightly sclerotized; plates average.

Anax walzinghami Mac Lachlan

MATERIAL STUDIED: One taken by Ottys and Ruth Sanders from Valles, Mexico; length 20, head width 4.7, wing cases 1. Although this is an immature specimen it appears to be this species according to the key given in Needham and Westfall 1955. (The length and width of the labium correspond to the description in the key although the median cleft is not as long as described.)

DENTAL FORMULA: 4 (F 10" to 13").

SHAPE OF PLATES: Apex approximately two-thirds distance from anterior to posterior end; apical angle in profile view equals 90° to 100°.

SIZE OF PLATES: Length 0.74; width 0.16.

SPINES: Graduated.

ARRANGEMENT OF SPINES: Largest at apex; smaller ones tending toward a line from apex to base on either side.

INTERCALARY FOLDS: Almost equal in width.

SCLEROTIZATION: Plates average, bases and intercalary folds not sclerotized.

Coryphaeschna ingens (Rambur)

MATERIAL STUDIED: One female from St. Tammany Parish, Louisiana, collected by A. Chaney and identified by G. H. Bick; length 50, head width 8, wing cases 12.

DENTAL FORMULA: 4 (F 6' to 7').

SHAPE OF PLATES: Apex about three-fourths distance from anterior to posterior end; in profile view, apical angle equals approximately 50°.

SIZE OF PLATES: Length 1.1; width 0.33.

SPINES: Almost uniform.

ARRANGEMENT OF SPINES: From apex in an irregular line toward base on either side.

INTERCALARY FOLDS: Equal in width.

SCLEROTIZATION: Plates average; bases and intercalary folds sclerotized lightly.

Nasiaeschna pentacantha (Rambur)

MATERIAL STUDIED: Two from St. Charles Parish, Louisiana, collected by J. Aycock and identified by G. H. Bick. One, length 50, head width 7, wing cases 12. One, length 26, head width 5, wing cases 3.5.

DENTAL FORMULA: 4 (F 5' to 12').

SHAPE OF PLATES: Apex about two-thirds distance from anterior to posterior ends; in profile view, apical angle equals about 100°.

SIZE OF PLATES: Length 1.1; width 0.33.

SPINES: Almost uniform.

ARRANGEMENT OF SPINES: Irregular cluster in apical region.

INTERCALARY FOLDS: Middle fold twice the width of lateral folds.

SCLEROTIZATION: Base and intercalary folds sclerotized; plates average.

Basiaeschna janata (Say)

MATERIAL STUDIED: Thirteen from Real (collected by Kirk Strawn and Clark Hubbs), Bell, and Hays counties. Five (three males and two females), length 30 - 35, head width 6.5 - 7, wing cases 9 - 10. One, length 25, wing cases 4. Four, length 20 - 22, head width 5, wing cases 2.5. One length 18, head width 4, wing cases 2. One, length 16, head width 4, wing cases 1. One, length 10, head width 2.5, wing cases 0.3.

DENTAL FORMULA: 4 (F 5' to 13').

SHAPE OF PLATES: Apex a little posterior to the middle of the plate; in profile view apical angle equals about 110°.

SIZE OF PLATES: Length 0.9 to 1.0; width 0.17.

SPINES: Graduated.

ARRANGEMENT OF SPINES: Grouped posterior to and around apex.

INTERCALARY FOLDS: Middle fold almost twice width of lateral folds.

SCLEROTIZATION: Plates average; flat bases and intercalary folds hardly

sclerotized.

VARIATION IN SPINE NUMBER: Of fifty-two plates, thirty-nine had from 7 to 10 spines; extremes were 5 and 14.

SEXUAL DIMORPHISM: Not present.

Epiaeschna heros (Fabricius)

MATERIAL STUDIED: Five collected by A. Chaney from Webster Parish, Louisiana (identified and given to me by G. H. Bick). Two, length 40, head width 9, wing cases 11; one, length 38, head width 8, wing cases 10; two, length 33, head width 6, wing cases 5.

DENTAL FORMULA: 4 (F 6' to 9').

SHAPE OF PLATES: Apex two-thirds distance from anterior end to posterior end of plate; apical angle equals 40° to 50° in profile view.

SIZE OF PLATES: Length 1.2; width 0.3.

SPINES: Almost uniform.

ARRANGEMENT OF SPINES: In somewhat of a row from apex to base on either side.

INTERCALARY FOLDS: Middle fold wider than lateral folds.

SCLEROTIZATION: Plates average; flat bases and intercalary folds lightly sclerotized.

WORK OF OTHER INVESTIGATORS

GENERA AND SPECIES STUDIED:

Aeshna grandis Linnaeus - Dufour 1852. An extremely small figure of the open proventriculus showing the armature. I believe that this figure is inaccurate, since the middle two plates do not resemble those of any family of Odonata studied.

Aeshna sp. - Schneider 1890. A drawing in color of part of the proventriculus showing four plates which are identical with one another. This may be attributable to the probability that the figure is diagrammatic, since in my work I have not found any proventriculus with four similar plates. The spines are fifteen in number with twelve arranged in pattern on the sides and anterior and posterior to the area that must be the apex. The number, arrangement, and size of spines differ from those of my Aeshna umbrosa Walker.

Aeshna sp. - Ris 1896. One proventricular plate of a half grown nymph. Since the ontogenetic development was not studied in this genus, a comparison cannot be made.

Aeshna sp. - Tillyard and Fraser 1938-1940. A row of seven spines arranged somewhat like those of my Aeshna umbrosa Walker, but the complete plate is not illustrated.

Aeshna sp. - Balfour-Browne 1944. This large figure emphasizes the intercalary folds which are almost similar to those of my Aeshna umbrosa Walker. However, the two do not agree as to the arrangement and number of spines.

Austroaeschna multipunctata Martin - Tillyard 1917. Figure small, but generally resembles my Aeshna umbrosa Walker in the number and arrangement of spines.

Anax sp. - Ris 1896. No figure. Statement that the armature is of the same type as in Aeshna.

Anax papuensis Burmeister - Tillyard 1917. Small figure, two views, showing two large spines in the apical region of the plates.

Anax imperator Leach - Barnard 1937. Very minute figures of two views of a single plate. Two small apical spines are present.

Anax junius (Drury) - Whedon 1919. No figures, but a description of the general appearance of the crop and the proventriculus is given.

SIGNIFICANCE:

The figures mentioned above of Anax papuensis Burmeister and Anax imperator Leach corroborate my conclusion that the proventricular armature is of importance in the taxonomy of the species of Anax.

ONTOGENETIC STUDIES

SPECIES STUDIED:

Boyeria vinosa (Say). Spines per plate in the two, thirteen, and fifteen millimeter nymphs range from 4 to 5 in number; in the twenty-five to twenty-nine millimeter nymphs from 3 to 5 in number.

Nasiaeschna pentacantha (Rambur). Spines per plate range in number from 8 to 12 in the twenty-six millimeter nymph; in a fifty millimeter nymph from 5 to 7 in number.

Basiaeschna janata (Say). Spines per plate range in number from 7 to 9 per plate in the ten millimeter nymph; from 7 to 10 in the sixteen millimeter nymphs; from 8 to 11 in the twenty to twenty-two millimeter nymphs; from 12 to 14 in the twenty-five millimeter nymph; and from 5 to 13 in the thirty to thirty-five millimeter nymphs.

SIGNIFICANCE:

There does not appear to be a correlation between spine number and the size of the nymph.

TABLE IV

Diagnostic Characteristics of the Aeshnidae

Name	Spines	(1)*	(2)*	(3)*	(4)*
Basiaeschna	5' - 13'	1/2+	2 X	110	Most of the spines are posterior to the apex.
Nasiaeschna	5' - 12'	2/3	2 X	100	Spines are very irregular in arrangement.
Coryphaeschna	6' - 7'	3/4	Equal	50	Spines very irregular in arrangement.
Aeshna	6' - 7'	2/3	Wider	100	Basal spines anterior to apical spines.
Boyeria	3' - 5'	2/3	Wider	100	Basal spines posterior to apical spines.
Epiaeschna	6' - 9'	2/3	Wider	40-50	Spines not as irregular as in Nasiaeschna, almost similar to Coryphaeschna.
Anax junius	2" - 3" plus 11"' - 23"'	2/3	Almost equal	70-105	Apical spines larger than other spines; spines on sides grouped in somewhat of a line from apex to base.
Anax walzinghami	10" - 13"	2/3	Wider	90-100	Intermediate between A. junius and A. amazili.
Anax amazili	10" - 15"	3/4	Almost equal	55	Spines scattered, of almost equal size.

* See next page for key to numbers (1) - (4).

(1) Distance apex is from anterior end of plate.

(2) Width of middle intercalary fold compared with lateral intercalary folds.

(3) Degrees in angle at apex as observed from lateral view.

(4) Additional characteristics.

PHYLOGENY

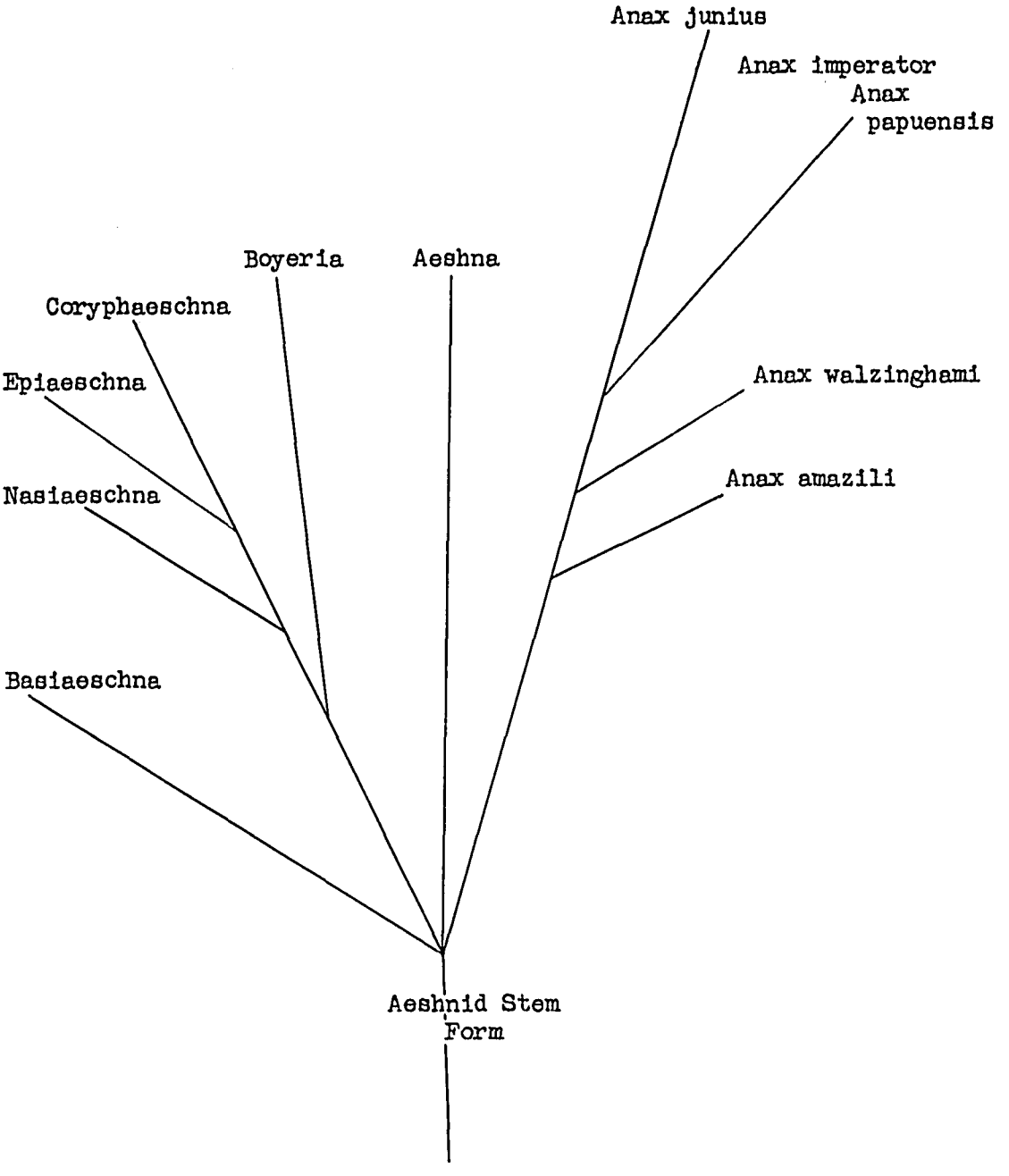


Figure 2. Phylogenetic relations of the Aeshnidae

TABLE V

Degrees of Specialization of the Aeshnidae

Species	Characteristics and Degree of Specialization*				
	I	II	III	IV	Total**
Basiaeschna janata	1	2	1	1	5
Nasiaeschna pentacantha	1	2	2	1	6
Coryphaeschna ingens	2	2	2	1	7
Epiaeschna heros	2	2	2	1	7
Anax junius	3	1	4 a	2	10
Anax walzinghami	1	2	2	1	6
Anax amazili	2	2	2	1	7
Aeshna umbrosa	1	2	3	1	7
Boyeria vinosa	1	2	3	1	7
Anax papuensis (Tillyard 1917)	1	3	4 b	2	10
Anax imperator (Barnard 1937)	1	3	4 b	2	10

* See list of characteristics and degrees of specialization.

** Total number represents the degree of specialization and is used in the accompanying phylogenetic chart.

PHYLOGENY

The relationships among the genera and species of Aeshnidae studied based on the structure of the proventricular armature are shown in the accompanying phylogenetic tree. The distance between the Aeshnid stem type and the genus or species represents the degree of specialization. The positions on the chart indicate the relations of the genera.

The degrees of specialization were derived from the accompanying chart and key. The Roman numerals refer to the general types of characteristics and the Arabic numbers represent the degrees of specialization.

SPECIALIZATION KEY

I. Height of raised area of plate.
   1. Low, apical angle wide.
   2. High, apical angle more acute.
   3. High, apical end a little skewed toward posterior.

II. Number of spines.
   1. Twelve to twenty-five.
   2. Five to fifteen.
   3. Two.

III. Arrangement of spines.
   1. Scattered on posterior half.
   2. Concentrated around apex.
   3. In a row to base on either side of apex.

4. a) Grouped on sides indicating lateral and median ridges.

4. b) Reduced to two apical spines.

IV. Size of spines.

1. Almost equal.

2. Laterals much reduced or absent.

DISCUSSION

According to the phylogenetic tree by Walker (1912). Boyeria, Epiaeschna, and Nasiaeschna form one of the two major branches with Basiaeschna and Aeshna on the other branch. He brings Coryphaeschna and Anax off of Aeshna with Anax as the most specialized genus of all of the Aeshnidae.

My study supports Walker's view that Anax is the most highly specialized genus of the Aeshnidae. The proventriculus does not offer any evidence in support of his idea that Anax is derived from Aeshna. However, the study of additional species of Aeshna might reveal interesting information.

The three species of Anax that I have studied and the two species that have had their armature figured in the literature do not exhibit common characteristics that are typical of the genus. There is greater diversity among the species of Anax than among the several other genera of Aeshnidae studied. However, the species of Anax fall into three groups as shown in the phylogenetic tree. Anax amazili appears to be the most primitive because of the scattered arrangement of the spines. Anax walzinghami has spines much like those of Anax amazili, but they seem to be arranged in somewhat of a line from apex to base on the sides. Anax junius has the lateral spines in groups forming indications of lateral

and median ridges from apex to base. All of the spines except the apical two or three are reduced in size. The apical area is slightly skewed toward the posterior end, but the spines are not particularly large. Anax imperator (Barnard 1937) and Anax papuensis (Tillyard 1917) have two large apical spines and apparently do not have other spines.

Walker's view of the Aeshna origin of Coryphaeschna is not substantiated by my study. The genus Coryphaeschna has armature much like that of Epiaeschna and somewhat like that of Nasiaeschna.

Boyeria and Aeshna are widely separated by Walker. The structure of their proventriculi does not support this view; however, their similarity may be the result of adaptive convergence rather than of similar origin, especially since the lower spines are more anterior in Boyeria than in Aeshna.

Basiaeschna appears to be the most primitive genus because of the arrangement of the spines, the width of the apical angle, and the position of the apex. The apex is a little posterior to the middle of the plate with the spines scattered on the posterior surface. The apical angle is the widest of the species studied. Walker also considers this genus as one of the most primitive.

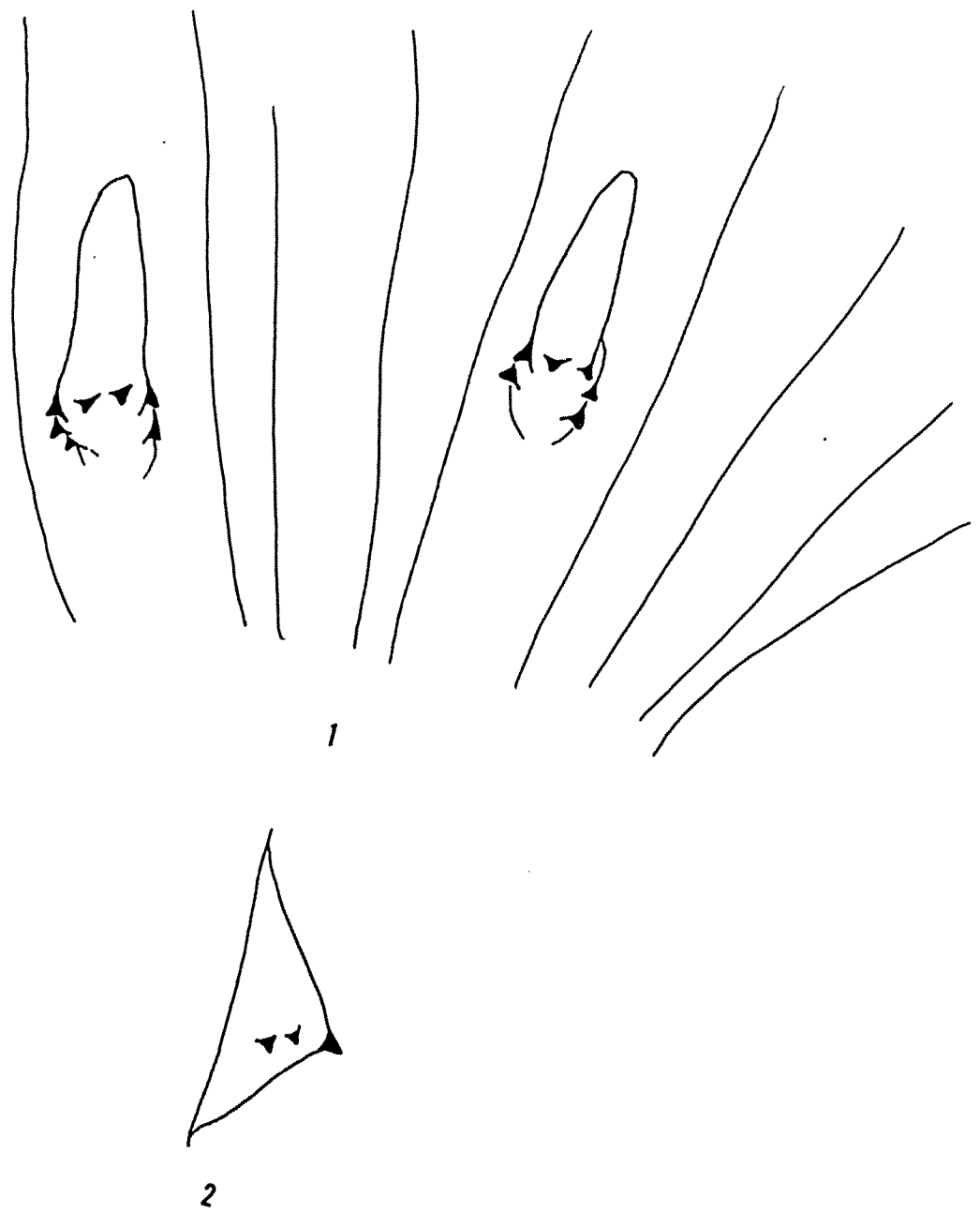
PLATE XV

Aeshna umbrosa

Figure 1. Ventral view of part of proventriculus showing two proventricular plates and six intercalary folds.

Figure 2. Lateral view of proventricular plate.

Scale: 2 cm. = 0.33 mm.



1

2

PLATE XVI

Boyeria vinosa

Figure 1. Proventricular plate of 27 mm. nymph.

Scale: 2 cm. = 0.33 mm.

Figure 2. Proventricular plate of 27 mm. nymph, two views.

Scale: 2 cm. = 1 mm.

Figure 3. Plate of 13 mm. nymph, two views.

Scale: 2 cm. = 0.33 mm.

1

2

3

PLATE XVII

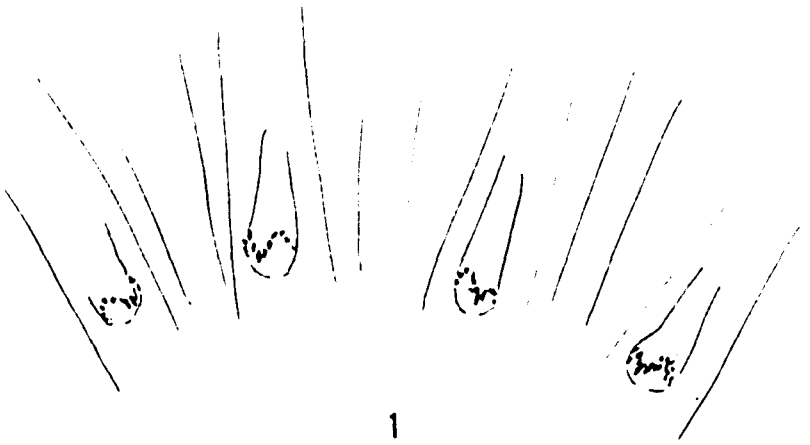
Anax junius

Figure 1. Proventricular plates and intercalary folds of a 43 mm. nymph.

Scale: 2 cm. = 1 mm.

Figure 2. Lateral view and surface view of one plate from a 43 mm. nymph.

Scale: 2 cm. = 0.33 mm.



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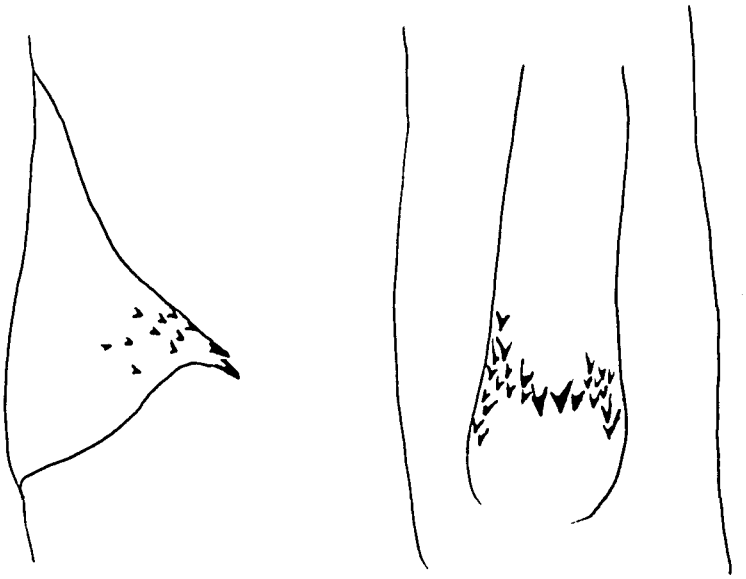


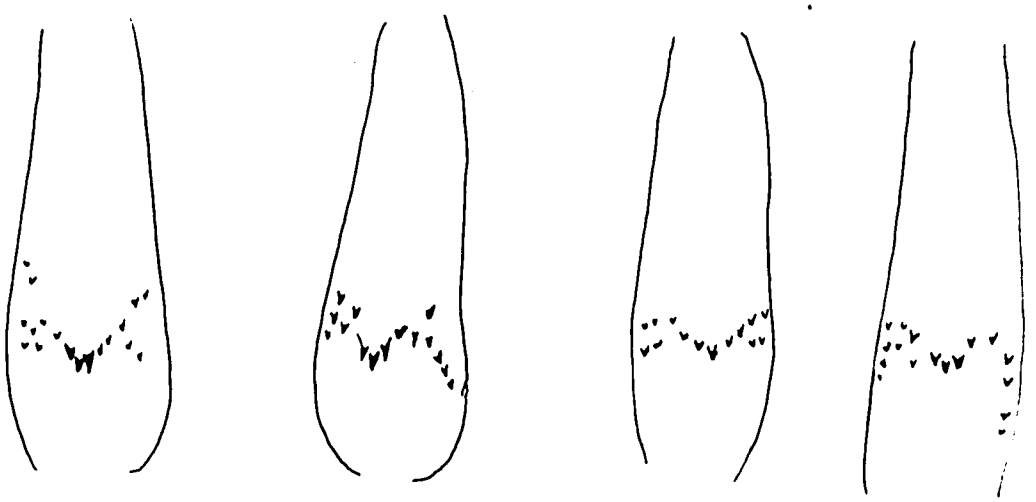
2

PLATE XVIII

Anax junius

Surface and lateral views of plates from different 43 mm. specimens to show variation. In each case the lower figure is the lateral view of the proventricular plate shown in the upper group.

Scale: 2 cm. = 0.33 mm.



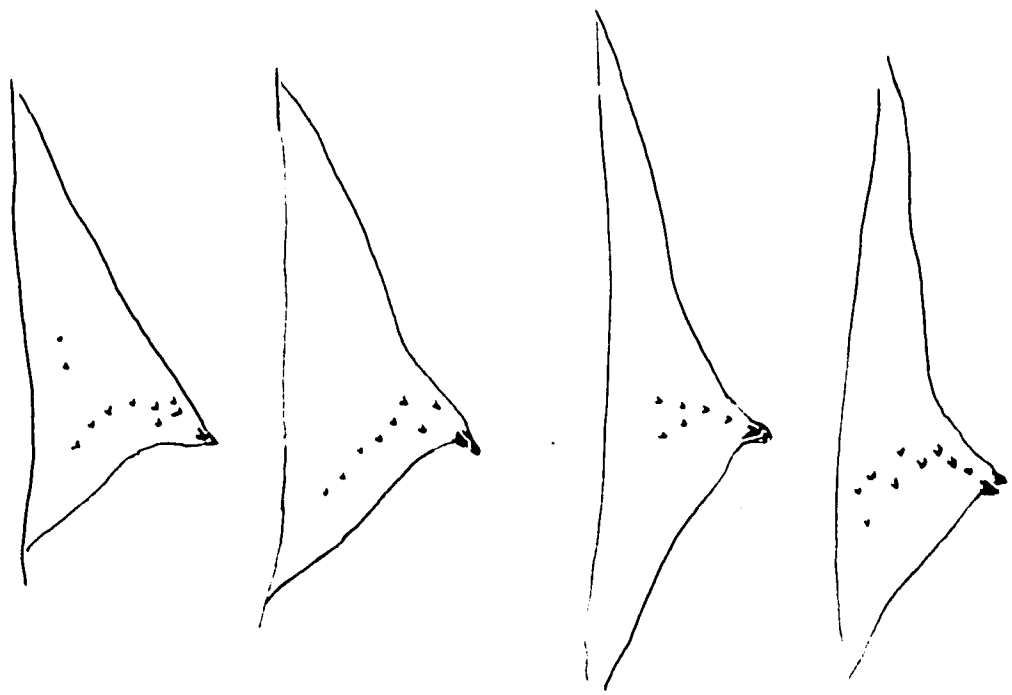


PLATE XIX

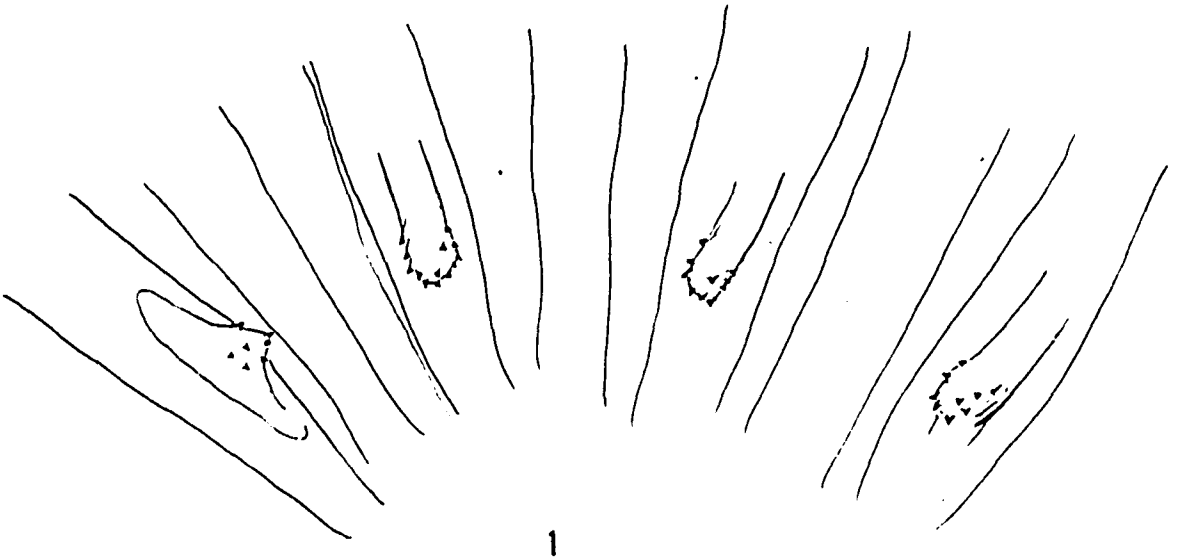
Anax amazili

Figure 1. Proventricular plates and intercalary folds of a 44 mm. nymph.

Scale: 2 cm. = 1 mm.

Figure 2. Lateral and surface views of one of the plates from the above specimen.

Scale: 2 cm. = 0.33 mm.



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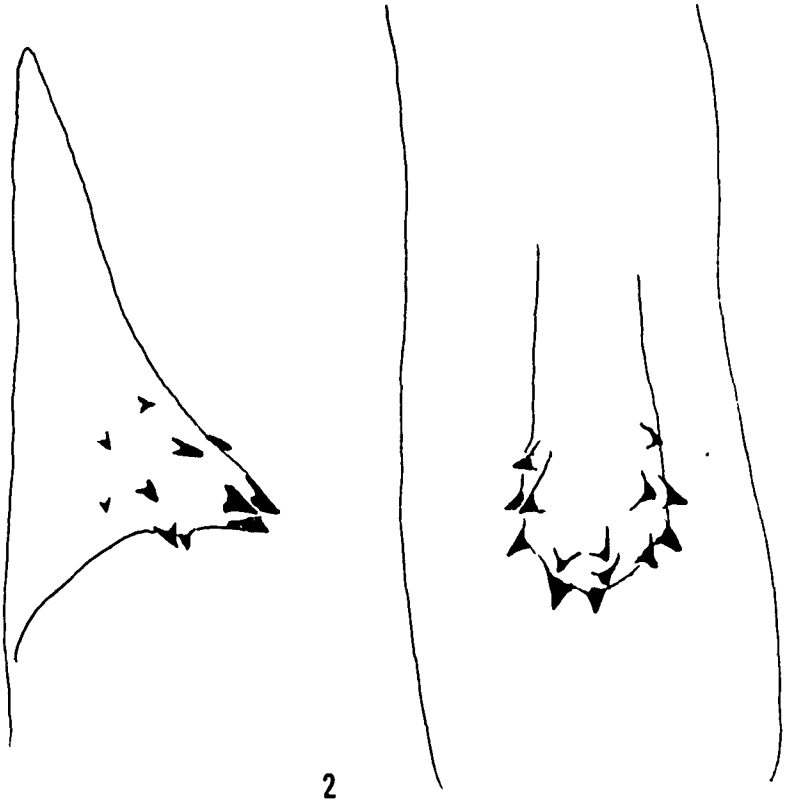


2

PLATE XX

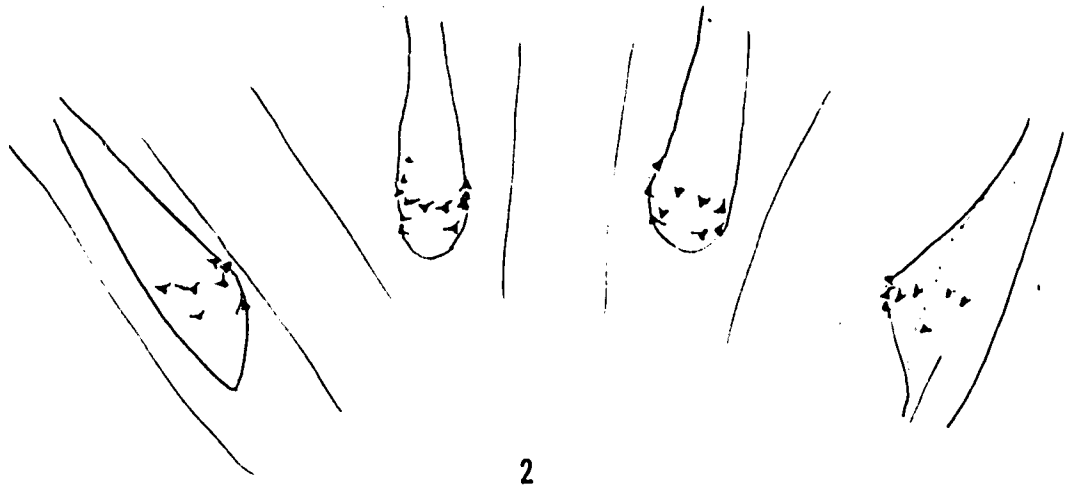
Anax amazili and *Anax walzinghami*

Figure 1. Proventricular plates of the 19 mm. *Anax amazili* from Mexico.

Figure 2. Proventricular plates from the 20 mm. *Anax walzinghami* from Mexico.

Scale: 2 cm. = 0.33 mm.

1



2

PLATE XXI

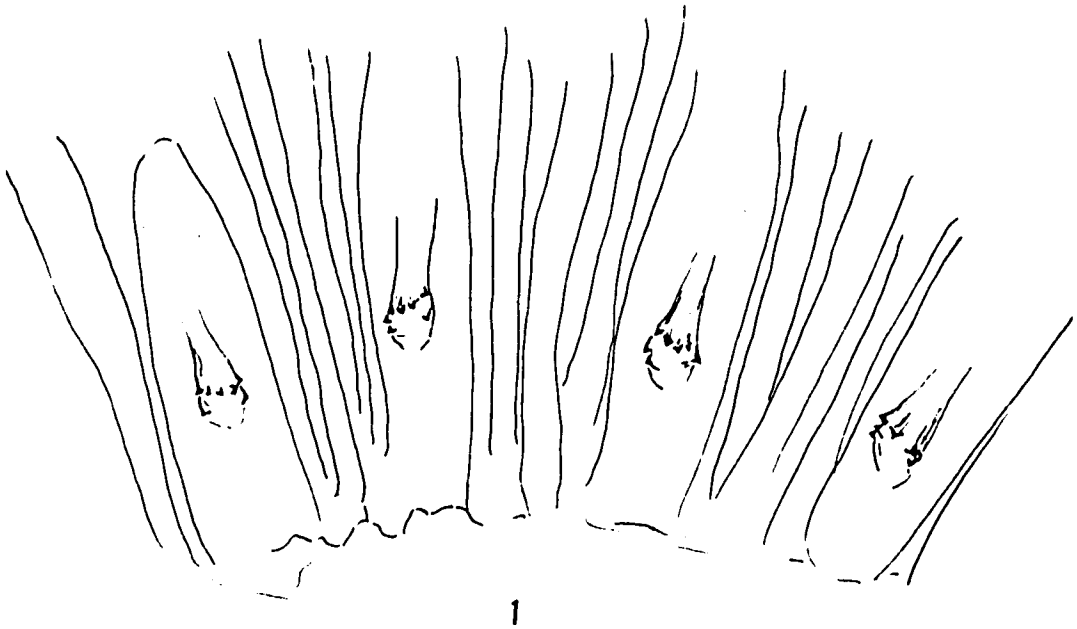
Coryphaeschna ingens

Figure 1. Section of proventriculus showing plates and intercalary folds.

Scale: 2 cm. = 1 mm.

Figure 2. Surface and lateral views of one of the plates from the above specimen.

Scale: 2 cm. = 0.33 mm.



1

2

PLATE XXII

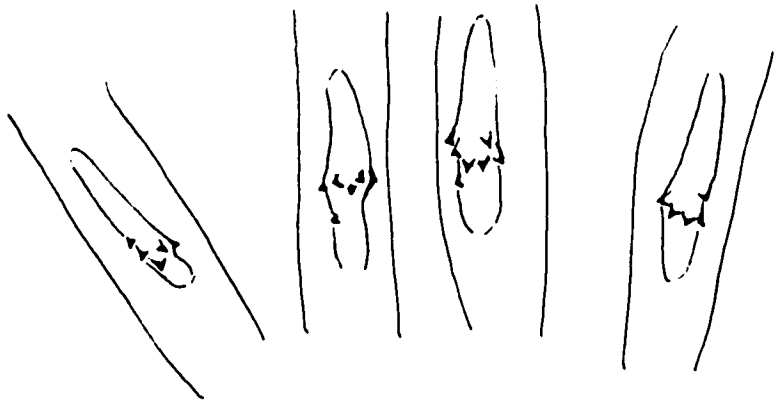
Nasiaeschna pentacantha

Figure 1. Proventricular plates of a 50 mm. nymph.

Scale: 2 cm. = 1 mm.

Figure 2. Surface and lateral views of one of the plates from the above specimen.

Scale: 2 cm. = 0.33 mm.



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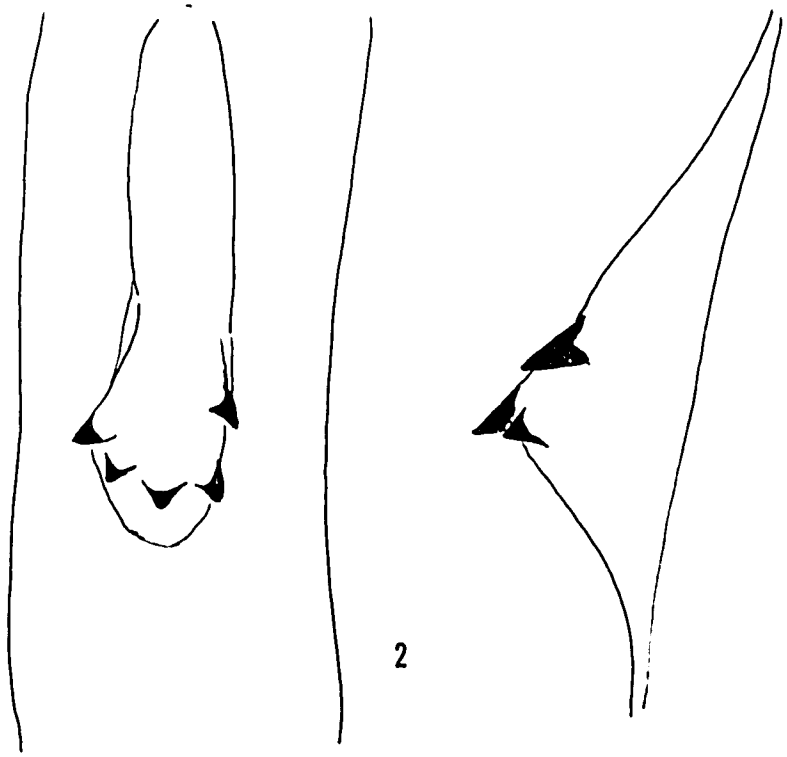

2

PLATE XXIII

Nasiaeschna pentacantha

Figure 1. Proventricular plates of a 26 mm. nymph.

Scale: 2 cm. = 1 mm.

Figure 2. Lateral view of one of the plates from the above specimen.

Scale: 2 cm. = 0.33 mm.

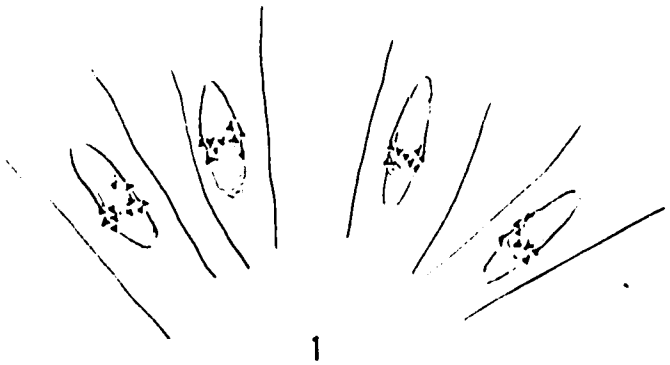

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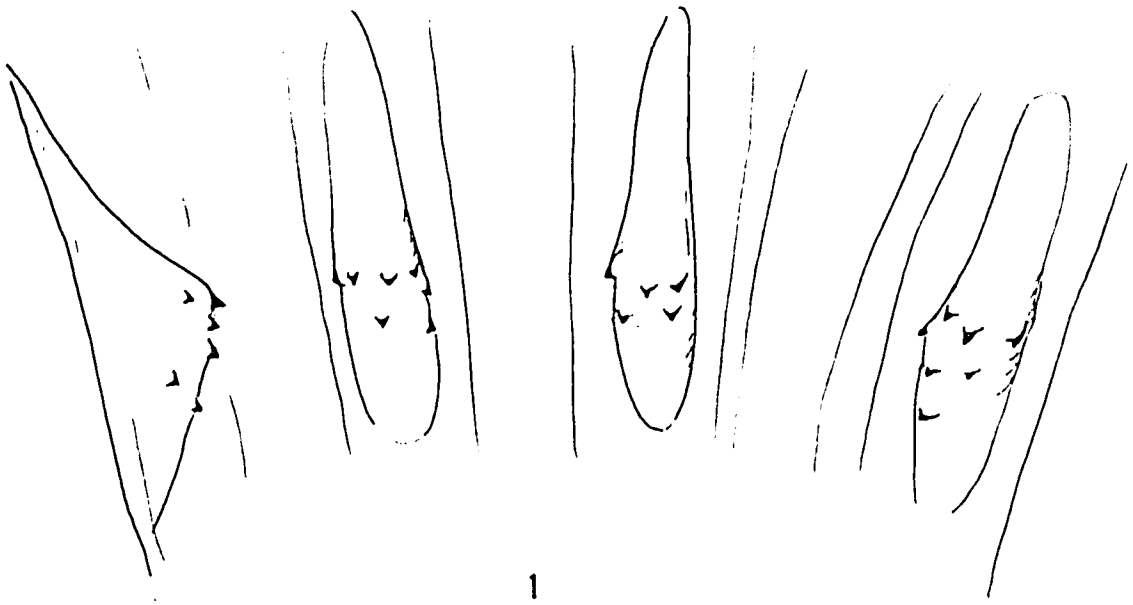
PLATE XXIV

Basiaeschna janata

Figure 1. Proventricular plates of a 35 mm. specimen. Scale: 2 cm. = 0.33 mm.

Figure 2. Lateral and surface views of plates from other numphs to show variation. From left to right: 33 mm. nymph, 33 mm. nymph, 25 mm. nymph, and 16 mm. nymph. Scale: 2 cm. = 0.33 mm.



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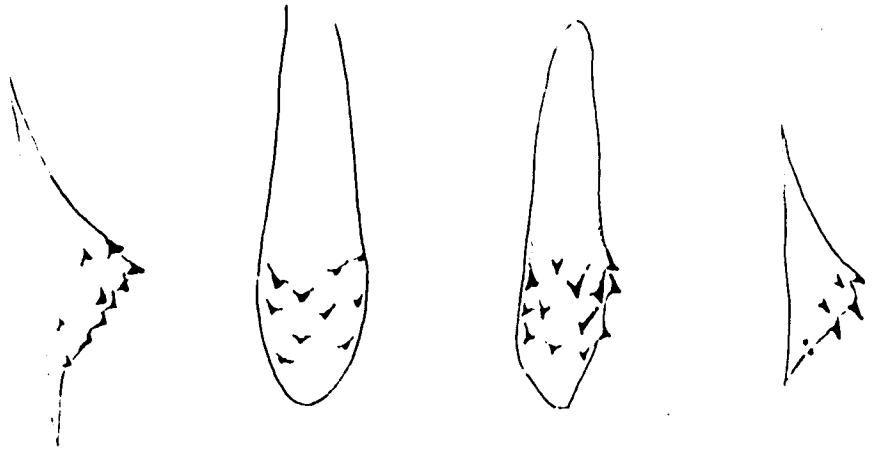


2

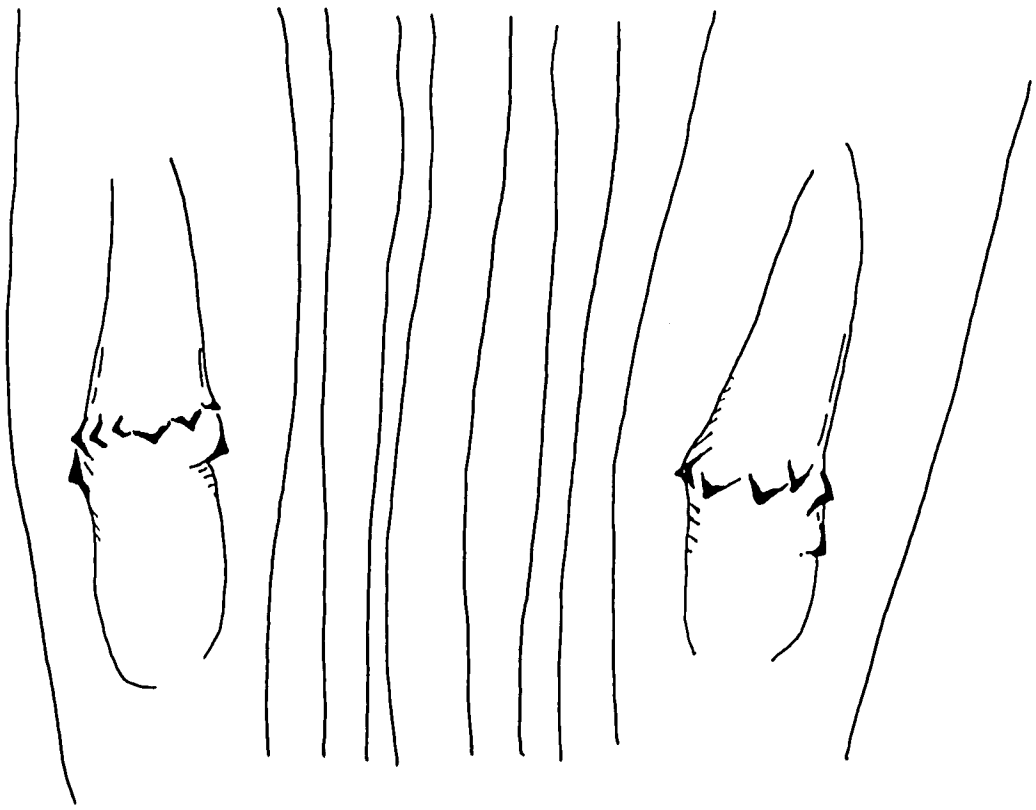
PLATE XXV

Epiaeschna heros

Figure 1. Two plates and three intercalary folds.

Figure 2. Lateral view of a plate.

Scale: 2 cm. - 0.33 mm.



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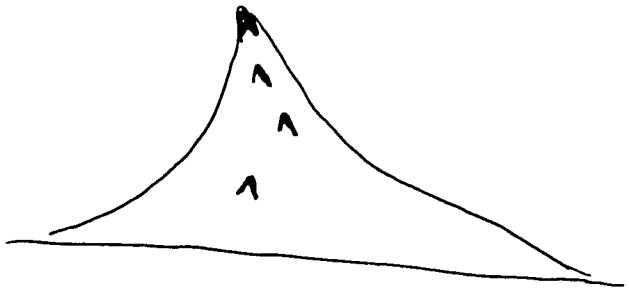


2

FAMILY CORDULEGASTERIDAE CALVERT

GENUS STUDIED

Cordulegaster Leach

CHARACTERISTICS OF THE GROUP

DENTAL FORMULA: 2 (F 1' + 6"-10"m, 7"-10"(+"')p) + 2 (F 1' + 7"-12"m,p).

SYMMETRY: Bilateral.

SHAPE OF PLATES:

a. Dorsal plates. Lateral surface of elevation large, resulting in lateral ridge reaching from apex to posterior end of base; median surface about one-half the size of lateral surface; flat bases oval with clearly defined margins.

b. Ventral plates. Lateral and median surfaces of elevated area equal in size; flat bases oval with clearly defined margins; apices slightly lateral to median line of plates.

SIZE OF PLATES: See species description.

SPINES: Apical spines fairly large; teeth on ridges very small. On the lower part of the lateral ridges of the dorsal plates there may be numerous minute spines.

ARRANGEMENT OF SPINES: On lateral and median ridges.

INTERCALARY FOLDS: Not sclerotized, indefinite.

SCLEROTIZATION: Plates well sclerotized.

Cordulegaster maculatus Selys

MATERIAL STUDIED: One female nymph collected by Robert Finch from McCurtain County, Oklahoma; length 45, head width 8, wing cases 10. Two collected by Kirk Strawn in Upshur County; length 20. Two collected by G. H. Bick from Cheboygan County, Michigan; length 17 and 20, head width 3 and 3.5, wing cases 0.5 and 1.0. All of these specimens keyed to C. maculatus in the book by Needham and Heywood (1929). On checking with the key in Needham and Westfall (1955), I questioned this identification; however, I could not decide upon a better identification. One of the Upshur County specimens differed from the other three specimens.

DENTAL FORMULA: As given for family.

SHAPE OF PLATES: As given for family.

SIZE OF PLATES: Length 0.85; width 0.33.

SPINES: As given for family. The lateral ridges of the dorsal plates of the largest specimen (Oklahoma) appeared to be without teeth; however, on closer examination with 45 X magnification, vestiges of teeth were observed. In the smaller specimens these ridges are toothed.

ARRANGEMENT OF SPINES: As given for family.

INTERCALARY FOLDS: As given for family.

WORK OF OTHER INVESTIGATORS

Cordulegaster sp., either C. annulatus or C. bidentatus - Ris 1896. A good figure of all four plates showing general form but not the exact number of teeth; much like my Cordulegaster.

Chlorogomphus sp. - Tillyard and Fraser 1938-1940. One proventricular plate. I assume that the dorsal plates in this genus differ from the ventral plates as they do in Orogomphus (as shown by Fraser 1925); however, this is not mentioned by Tillyard and Fraser.

Orogomphus campioni and O. atkinsoni (Fraser 1925). Dorsal and ventral plates figured for each species.

The genera Chlorogomphus and Orogomphus, according to Tillyard (1917), make up the subfamily Chlorogomphinae, which he included with the Gomphinae, Petalurinae, Cordulegasterinae, and Aeshninae in the family Aeshnidae. Fraser in 1925 considered the Chlorogomphinae as a subfamily with the Cordulegasterinae in the family Cordulegasteridae. As evidence to support this view, he said the proventricular armature was "typically Cordulegasterine in shape." Neither a figure nor a description of the "typical Cordulegasterine" type was included; therefore, there is a possibility that he did not make sufficient study of the two forms to note the significance of the differences. The following table gives a summary of the contrasting characteristics resulting from a comparison of the above mentioned figures of the Chlorogomphines with my Cordulegaster specimens and Ris' figure of Cordulegaster sp.

TABLE VI

Comparison of the Proventricular Plates of

Cordulegaster and Chlorogomphines

Structure	Cordulegaster	Chlorogomphines
Median and lateral surfaces of elevated areas.	Ventral Plates: Equal. Dorsal Plates: Lateral is much larger than median.	Equal on both pairs of plates.
Surface spines.	Absent on all plates.	Absent on one pair of plates.
Teeth.	On median and lateral ridges of all four plates, but mere vestiges on lateral ridge of 45 mm. specimen.	On median and lateral ridges of all four plates.
Position of apex.	At or a little posterior to the middle of plate.	At or posterior to the posterior end of plate.

From my comparison of these two groups of relatively archaic Odonata, I postulate that each might eventually be elevated to family rank. Upon checking their venation as given by Needham (1903) and finding that of the Chlorogomphines unique, I believe that further study of the morphology of these two groups may reveal sufficient dissimilarities to corroborate the above statement.

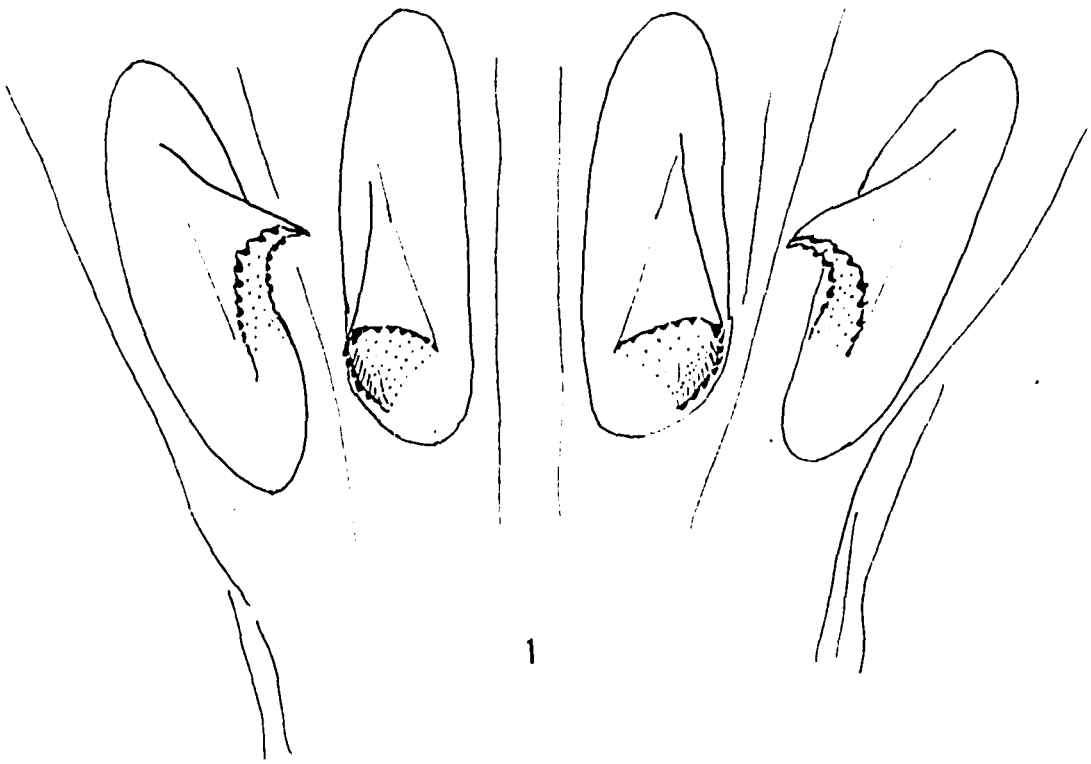
PLATE XXVI

Cordulegaster maculatus

Figure 1. Ventral view of open proventriculus showing plates of a 20 mm. nymph.

Figure 2. Dorsal plate from the 45 mm. nymph.

Scale: 2 cm. = 1 mm.



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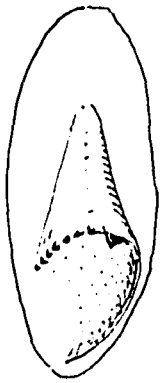


2

PLATE XXVII

Cordulegaster maculatus

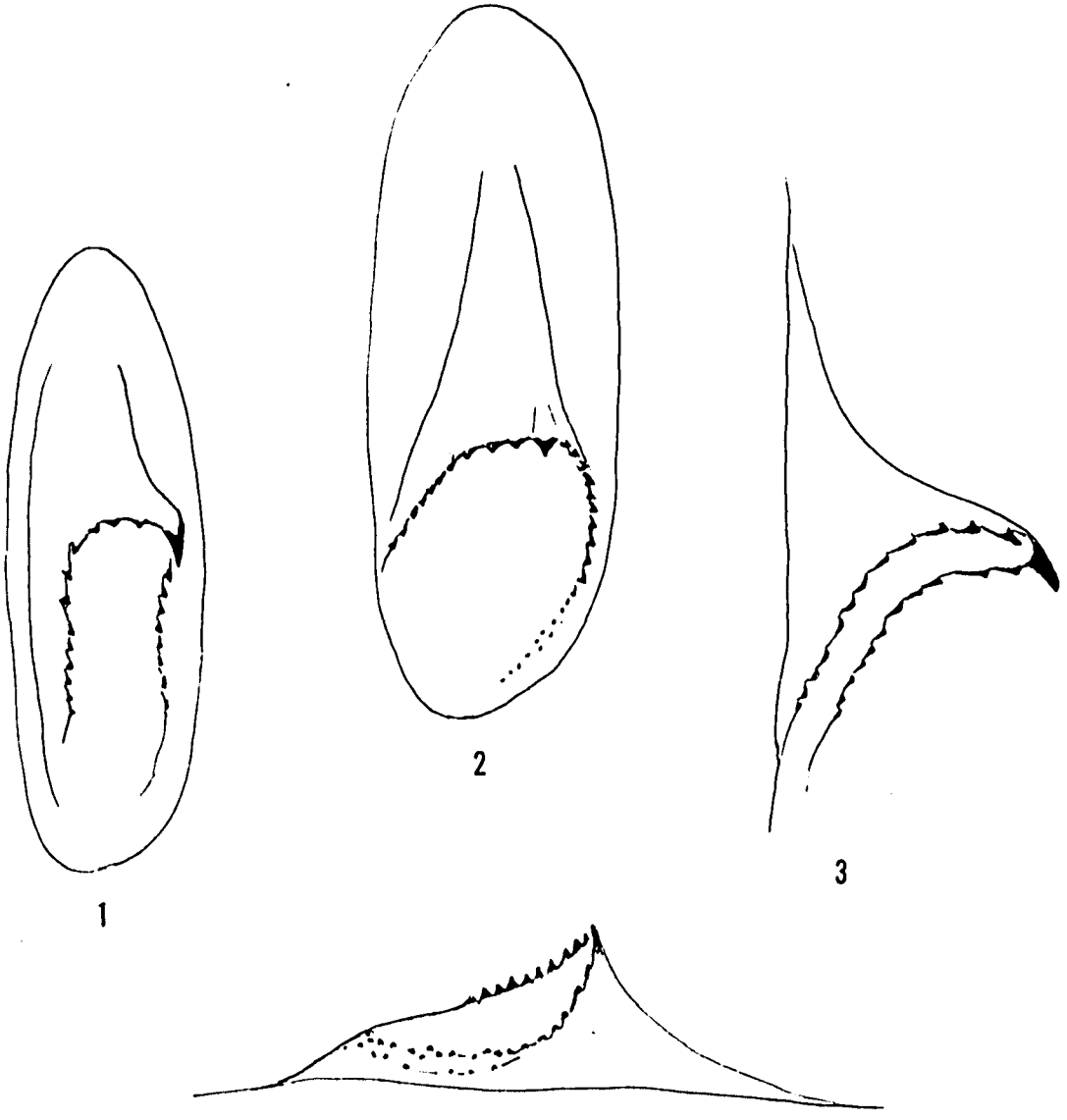
Figure 1. Right ventral plate of 20 mm. nymph, surface view.

Figure 2. Right dorsal plate of 20 mm. nymph, surface view.

Figure 3. Right ventral plate of 20 mm. nymph, lateral view.

Figure 4. Right dorsal plate of 20 mm. nymph, lateral view.

Scale: 2 cm. = 0.33 mm.


1
2
3
4

FAMILY LIBELLULIDAE RAMBUR

GENERA STUDIED

Macromiinae Needham

- Didymops Rambur
- Macromia Rambur

Corduliinae Selys

- Tetragoneuria Hagen
- Epicordulia Selys
- Somatochlora Selys
- Neurocordulia Selys

Libellulinae Selys

- Erythemis Hagen
- Lepthemis Hagen
- Libellula Linnaeus
- Plathemis Hagen
- Orthemis Hagen
- Sympetrum Newman
- Pachydiplax Brauer
- Dythemis Hagen
- Brechmorhoga Kirby
- Perithemis Hagen
- Paltothemis Karsch
- Pantala Hagen
- Tramea Hagen

CHARACTERISTICS OF THE GROUP *

DENTAL FORMULA: 2 (F 1" + 3"-9"m) + 2 (F 2' + 0"'-7"'p).

SYMMETRY: Bilateral.

SHAPE OF PLATES: Almost uniform for all Libellulidae studied.

a. Dorsal plates. Base flat with almost parallel lateral and median margins and rounded anterior margin; elevated area with lateral surface reduced in size; apex low, near lateral margin at or anterior to middle of plate; toothed median edge long, extends from apex between the wide but flattened lateral and posterior surfaces to the base in the posterior quadrant of the plate.

---

*NOTE: Three exotic genera, Presba, Synthemis, and Cordulephya whose proventricular plates have been figured by Barnard (1937), Tillyard (1910), and Tillyard (1917) respectively, are not considered in the group characterized, but will be discussed later in the section on phylogeny. They seem to be intermediate forms, more primitive than the Macromiinae and Corduliinae (sensu strictu).

b. Ventral plates. Base oval; elevated apex skewed laterally, median surface greatly expanded and flat; lateral surface reduced; posterior surface narrow with the edges between it and the sides almost parallel, the lateral edge forming the posterior margin of the plate; two large spines are present pointing in a posterior direction, one at the apex and the other anterior to it on the line between the apex and the anterior end of the plate. There is no separate flattened base.

SIZE OF PLATES: Ventral plates usually larger than dorsal plates.

ARRANGEMENT OF SPINES:

a. Dorsal plates. On the median ridges there are 4 to 10 teeth.

b. Ventral plates. Two large spines one at the apex and one anterior to the apex. In the Macromiinae tiny teeth are present on the lateral ridges (p).

INTERCALARY FOLDS: Between dorsal plates there are three lightly sclerotized folds. The middle fold is three times as wide as the lateral folds, which are almost continuous with the dorsal plates. Between the other plates the folds are irregular and unsclerotized.

SCLEROTIZATION: Variable.

DESCRIPTIONS OF PROVENTRICULAR ARMATURE OF SPECIES

Didymops transversa (Say)

MATERIAL STUDIED: Nine from Dallas, Bexar, and Bastrop (collected by Kirk Strawn and Clark Hubbs) counties. Two, length 26, head width 7, wing cases 9; one, length 23, head width 5.5, wing cases 4; two, length 21, head width 5 - 5.5, wing cases 4.5 - 4.7; three, length 11 - 13,

head width 2.5 - 3, wing cases 0.5 - 1.0.

DENTAL FORMULA: 2(F 4" to 9" m) + 2 (F 2' + 4"' to 9"' p).

SIZE OF PLATES: Dorsal plates, length 1.6, width 0.75; ventral plates, length 2.2, width 0.75.

VARIATION IN SPINE NUMBER: Of sixteen dorsal plates tabulated, twelve had from 6 to 8 teeth; extremes were 4 and 9. Of sixteen ventral plates tabulated, ten had from 6 to 8 teeth; extremes were 4 and 9. One ventral plate of an eleven millimeter nymph had an extra spine on the anterior, or non-apical spine.

Macromia caderita Needham

MATERIAL STUDIED: One from Hays County collected by Kirk Strawn; length 25, head width 8, wing cases 10.

DENTAL FORMULA: 2 (F 9" m) + 2 (F 2' + 7"' p).

SIZE OF PLATES: Dorsal plates length 2.3, width 0.8; ventral plates, length 2.7, width 0.1.

Tetragoneuria sp.

MATERIAL STUDIED: One large nymph from Real County taken by Kirk Strawn and Clark Hubbs.

DENTAL FORMULA: 2 (F 6" m) + 2 (F 2').

SIZE OF PLATES: Dorsal plates, length 1.2, width 0.6; ventral plates, length 1.5, width 0.5.

Epicordulia princeps (Hagen)

MATERIAL STUDIED: Nymphs were collected by Billy T. Jones in Hays County; ten, length 25, head width 6, wing cases 8; one, length 12, head width 3.7, wing cases 1; one, length 10, head width 3, wing cases 0.7; and one, length 7.5, head width 2, wing cases 0.3.

DENTAL FORMULA: 2 (F 4" to 6" m) + 2 (F 2').

SIZE OF PLATES: Dorsal plates, length 1.5, width 0.8; ventral plates, length 1.7, width 0.7.

VARIATION IN SPINE NUMBER: Of eighteen dorsal plates tabulated, thirteen had 5 teeth each; extremes were 4 and 6.

Somatochlora linearis (Hagen)

MATERIAL STUDIED: One from Jackson Parish, Louisiana, collected and identified by G. H. Bick; length 23, head width 6, wing cases 9.5.

DENTAL FORMULA: 2 (F 6" to 7" m) + 2 (F 2').

SIZE OF PLATES: Dorsal plates, length 1.7, width 1.0; ventral plates, length 2.5, width 0.7.

Neurocordulia molesta (Walsh)

MATERIAL STUDIED: One from Bowie County, collected by Kirk Strawn and Clark Hubbs; length 20, head width 6, wing cases 4. The profile view of the dorsal spines is not similar to that given in the photograph (page 356) by Needham and Westfall (1955) of N. molesta, but more like the figure given by Byers (1937) if the specimen he called Platycordulia xanthosoma

(by supposition) which was later found to be N. molesta.

DENTAL FORMULA: 2 (F 7" m) + 2 (F 2').

SIZE OF PLATES: Dorsal plates, length 1.2, width 0.5; ventral plates, length 1.7, width 0.5.

Erythemis simplicicollis (Say)

MATERIAL STUDIED: Seven collected from Dimmit, Tom Green, and Real counties; length 15 to 17, head width 5, wing cases 7 to 8. Five from Hays County; one, length 6.5, head width 2, wing cases 0.5; one, length 7, head width 2.7, wing cases 0.5; two, length 8, head width 3, wing cases 1; one, length 11, head width 3, wing cases 1.5.

DENTAL FORMULA: 2 (F 5" to 6" m) + 2 (F 2').

SIZE OF PLATES: Dorsal plates, length 1.5, width 0.75; ventral plates, length 2, width 0.75.

Lepthemis vesiculosa (Fabricius)

MATERIAL STUDIED: One large nymph from Uvalde County:

DENTAL FORMULA: 2 (F 5" to 6" m) + 2 (F 2').

SIZE OF PLATES: Dorsal plates, length 1.5, width 0.8; ventral plates, length 2.1, width 0.9.

Libellula auripennis Burmeister

MATERIAL STUDIED: Two from Morris County; length 22, head width 5.5, wing case 8. These specimens keyed to this species in C. F. Byers' 1927 key with G. H. Bick's 1951 addition. However, I am not certain that they are correctly identified.

DENTAL FORMULA: 2 (F 6" to 7" m) + 2 (F 2').

SIZE OF PLATES: Dorsal plates, length 1.2, width 0.75; ventral plates, length 2.0, width 0.7.

Plathemis lydia (Drury)

MATERIAL STUDIED: Six collected from Bandera and Real counties by Kirk Strawn; length 21, head width 5, wing cases 7.

DENTAL FORMULA: 2 (F 6" to 8" m) + 2 (F 2').

SIZE OF PLATES: Dorsal plates, length 1.2, width 0.75; ventral plates, length 1.7, width 0.7.

Orthemis ferruginea Fabricius

MATERIAL STUDIED: Six from Bell, Aransas, Hardin, San Patricio, and McLennan counties; length 22 - 23, head width 5.5 - 6.5, wing cases 6 - 9.

DENTAL FORMULA: 2 (F 5" to 9" m) + 2 (F 2').

SIZE OF PLATES: Dorsal plates, length 1.2, width 0.7; ventral plates, length 2.0, width 0.7.

VARIATION IN SPINE NUMBER: Of the twelve dorsal plates, five had 6 teeth; extremes were 5 and 9.

Sympetrum vicinum (Hagen)

MATERIAL STUDIED: Two from Kerr County; length 14, head width 4, wing cases 5.

DENTAL FORMULA: 2 (F 4" to 6" m) + 2 (F 2').

SIZE OF PLATES: Dorsal plates, length 1.0, width 0.5; ventral plates, length 1.2, width 0.33.

VARIATION IN SPINE NUMBER: Three of the four dorsal plates examined had 6 teeth each.

Pachydiplax longipennis Burmiester

MATERIAL STUDIED: Five females from Morris and Harrison counties; length 16 - 17, head width 4, wing cases 6.

DENTAL FORMULA: 2 (F 6" to 7" m) + 2 (F 2').

SIZE OF PLATES: Dorsal plates, length 1.0, width 0.33; ventral plates, length 1.5, width 0.5.

Dythemis sp.

MATERIAL STUDIED: One from Bastrop County; length 20, head width 4, wing cases 5.

DENTAL FORMULA: 2 (F 5" m) + 2 (F 2').

SIZE OF PLATES: Dorsal plates, length 1.0, width 0.7; ventral plates, length 1.7, width 0.6.

Brechmorhoga mendax Hagen

MATERIAL STUDIED: Eight (four males and four females) from Irion and Hays counties taken by Kirk Strawn and Clark Hubbs; length 23 - 24, head width 5.5, wing cases 8.

DENTAL FORMULA: 2 (F 4" to " m) + 2 (F 2').

SIZE OF PLATES: Dorsal plates, length 1.0, width 0.7; ventral plates, length 2.0; width 0.5.

SEXUAL DIMORPHISM: Not present.

VARIATION IN SPINE NUMBER: Of sixteen dorsal plates, eleven had 6 to 7 teeth.

Perithemis tenera (Say)

MATERIAL STUDIED: Four from Tom Green, Hardin, Palo Pinto, and Anderson counties; length 12 - 15, head width 3.5 - 4, wing cases 5.

DENTAL FORMULA: 2 (F 4" to 6" m) + 2 (F 2').

SIZE OF PLATES: Dorsal plates, length 0.7, width 0.5; ventral plates, length 1.2, width 0.4.

Paltothemis lineatipes Karsch

MATERIAL STUDIED: Five taken by Ottys and Ruth Sanders from Jeff Davis County; length 24, head width 7, wing cases 10.

DENTAL FORMULA: 2 (F 7" to 10" m) + 2 (F 2').

SIZE OF PLATES: Dorsal plates, length 1.5, width 1.0; ventral plates, length 2.0, width 0.7.

Pantala hymenea (Say)

MATERIAL STUDIED: Five mature nymphs from Bandera, Bastrop, Dallas, and Uvalde counties.

DENTAL FORMULA: 2 (F 4" to 6" m) + 2 (F 2').

SIZE OF PLATES: Dorsal plates, length 1.7, width 0.8; ventral plates, length 2.2, width 1.0.

Tramea sp.

MATERIAL STUDIED: One mature nymph from Dallas County; length 2.3, head width 6, wing cases 8.

DENTAL FORMULA: 2 (F 4" m) + 2 (F 2').

WORK OF OTHER INVESTIGATORS

GENERA AND SPECIES STUDIED:

Presba venator Barnard - Barnard 1937. Small figure showing two plates.

Cordulephya pygmaea Selys - Tillyard 1917. Small figure showing two plates.

Synthemis eustalacta (Burmeister) - Tillyard 1910. A description and figure showing all four plates.

Macromia picta Selys - Barnard 1937. No figures. According to Barnard, this species has armature similar to that of Presba venator. However, the members of the Macromiinae that I have studied have proventricular plates that differ in several ways from those of Presba.

Epophthalmia sp. - Ris 1896. No figures. According to Ris, this genus has armature similar to Cordulia sp. Since in the Macromiinae that I have examined the toothed condition of the lateral ridges of the ventral plates appears to be a subfamily characteristic, I assume that in this genus the teeth were also present, the significance of which fact was not noted by Barnard.

Cordulia sp. - Ris 1896. Small figure.

Diplax sp. and Libellula sp. - Ris 1896. No figures. Statement by Ris that these genera have the same type of armature as Cordulia. Since Cordulia is a higher Corduliine in the group with Neurocordulia, et al that I have studied, my work corroborates this opinion.

Libellula depressa Linnaeus - Dufour 1852. Poor figure.

Orthemis ferruginea Fabricius and Erythemis plebeja Burmeister - Calvert 1927. He said that their proventricular plates are similar to Ris' Cordulia.

Pseudomacromia torrida Kirby - Barnard 1937. Small figure.

Crocothemis sp., Helothemis sp., Orthetrum sp. - Barnard 1937. No figures given. Barnard said that these genera have plates of similar structure, and very briefly characterized those of Orthetrum.

Sympetrum sp. - Balfour-Browne. Good drawing showing one dorsal and one ventral plate.

SIGNIFICANCE:

The figures of Presba, Cordulephya, and Synthemis are important since these genera are intermediate forms. They are discussed in the section on general phylogenetic considerations.

The differences between the Macromiinae and the related groups evidently were not heretofore noticed.

My work corroborates the opinion that the higher Corduliines and the Libellulinae have the same type of armature, but in this study I have checked the minute differences among genera and the intra-generic variations in the higher Corduliines and the Libellulinae.

ONTOGENETIC STUDIES

SPECIES STUDIED:

Didymops transversa (Say). Dorsal Plates: In three, eleven to thirteen millimeter nymphs the teeth ranged from 4 to 7 in number. In three, twenty-one to twenty-three millimeter nymphs, they ranged from 6 to 9. The twenty-six millimeter numphs had 7 to 9 teeth. Ventral Plates: In three, eleven to thirteen millimeter nymphs the teeth ranged from 4 to 6; in three, twenty-one to twenty-three millimeter nymphs the teeth ranged from 6 to 8; in one, twenty-six millimeter specimen the teeth were 9 in number on both plates.

Epicordulia princeps (Hagen). In one seven and one-half millimeter nymph, the dorsal plates had 6 and 5 teeth each; one, ten millimeter nymph had 4 teeth on each dorsal plate; one twelve millimeter nymph had 4 and 5 teeth on the dorsal plates. Ten, twenty-five millimeter nymphs had 5 to 6 teeth on their dorsal plates.

Erythemis simplicicollis (Say). One nymph six and one-half millimeters long had 6 and 5 teeth on its dorsal plates; one, seven millimeter nymph had 6 teeth on each of its dorsal plates. One, eight millimeter nymph had 5 on each of its plates and another had 5 and 6 teeth. An eleven millimeter nymph had 6 teeth on each of its dorsal plates. The seven, fifteen to seventeen millimeter nymphs had 5 to 6 teeth on their dorsal plates.

SIGNIFICANCE:

There does not appear to be a correlation between the number of

teeth on the dorsal plates and the size of the nymph.

In the Macromiine, Didymops transversa (Say), which have tiny teeth on the lateral ridges of the ventral plates, the data indicate that there might be a correlation between the number of teeth and the age of the nymph. Additional material should be checked before a conclusion can be reached.

In the eleven millimeter nymph of the Didymops an extra spine was present on the anterior spine of the ventral plate. This spine looked like the one in the figure of Presba (Barnard 1937). Additional Macromiines of this size or smaller should be checked to determine whether this is a freak or occurs frequently. It may represent a palingenetic characteristic that has normally disappeared in the Macromiinae and the Libellulidae.

TAXONOMY AND PHYLOGENY OF THE LIBELLULIDAE

The proventricular armature of the genera of Corduliinae and Libellulidae studied are much alike. The differences that appear to be characteristic of the genera are differences in degree of development rather than in form of structure; therefore, they are intangible for use in descriptions. The accompanying table summarizes the characteristics that appear to be the most significant for the genera.

The shape of the apical spines of the ventral plates as seen in profile view (Plate L) appears to be one of the better of the characters for taxonomic purposes. However, they show much variation within a species. In some specimens they are low and appear to be well worn. In this study the longest and most pointed spines are considered to be typical for the species.

The grouping of the genera according to the characteristics of the proventricular armature is very difficult. Erythemis and Lepthemis, however, are much alike. They both have an extra convexity in the lateral ridge of the ventral plates; the base of each spine is relatively thick; and the plates are less angular (more "heavy set") in appearance. The affinities of the other genera studied are less pronounced than those of the above. Sympetrum, Pachydiplax, Libellula, Orthemis, and Plathemis appear to be related because of the poor development of the beak-like prolongation and the shape of the posterior angle of the end of the apical spine of the ventral plates.

Paltothemis, Pantala, and Tramea have well developed and uptilted

beak-like extensions of the apical spines of the ventral plates, and in general appearance the plates are somewhat alike. However, Paltothemis has a greater number of teeth on the dorsal plates than do Pantala and Tramea.

Dythemis, Brechmorhoga, and Perithemis have apical spines that resemble each other; however, the dorsal plates of Perithemis are wider in proportion to their length than are those of Brechmorhoga and Dythemis.

The arrangement of genera based on the proventricular armature alone as given in the preceding paragraphs lends support to the system proposed by Needham and Broughton (1927) rather than to the arrangement of these genera by Ris (1909 - 1916). I placed Perithemis with Dythemis and Brechmorhoga because of the shape of the apical spines; however, the proportions of the dorsal plates must, in this case, be of greater importance in showing its affinities since their form corroborates the isolation of this genus as given by Ris and by Needham and Broughton. My grouping of Paltothemis with Tramea and Pantala differs only to a small degree from Needham and Broughton's arrangement. They have it with Brechmorhoga and Dythemis, but close to Tramea in a linear series.

TABLE VII

Characteristics of the Genera of Libellulidae

Genus	Key Number *								
	1	2	3	4	5	6	7	8	9
Erythemis	2-	1+	5-6	1	3	2.2	2-	1	1
Lepthemis	2+	2+	5	1				1	
Libellula	2+	1+	6-7	2	2	1.5	2-	2	1
Plathemis	2+	1+	6-8	2	3	1.7	2-	2	1
Orthemis	2+	1+	5-9	3	3	1.7	2+	2	1
Sympetrum	2	1	6	3				1	
Pachydiplax	1+	1+	6-7	1	4	2.0		1	1
Dythemis	2+	1+	5					2	
Brechmorhoga	2+	1	4-8	4	2	1.2	2-	2	3
Perithemis	3-	1-	4-6	4	2	2.2	2-	1	1
Paltothemis	2+	1+	7-10	4	1	2	2-	1	1
Pantala	2-	2-	4-6	4	1		2-	3	2
Tramea			4	4				3	
Epicordulia	2+	2+	5						
Neurocordulia	1+	1+	7						
Somatochlora	2-	1+	6-7						
Tetragoneuria	2	2+	6						

*NOTE:

1. Ratio in fourths between width and length of the dorsal plates.
2. Ratio in fourths between width and length of the ventral plates.
3. The number of teeth per dorsal plate.
4. Relative lengths of beak-like projections of terminal spines of

ventral plates as observed from profile view.

5. Relative size of solid-cap-like area of apical spines of ventral plates as seen in profile view.
6. Ratio in thousanths between height of plates and body length.
7. Ratio in fourths between height of apex of dorsal plates and length of lateral side of elevated area.
8. Relative lengths of anterior spines of ventral plates.
9. Relative lengths of ridges extending from the anterior spines of ventral plates.

PLATE XXVIII

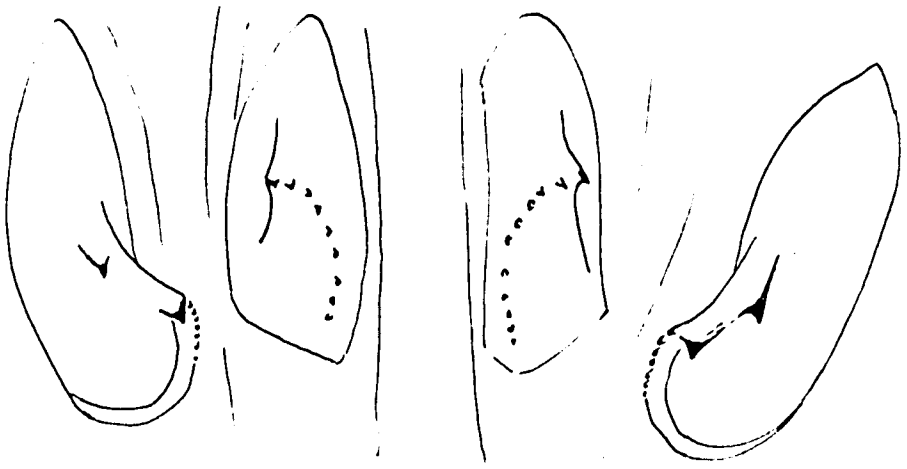
Macromia caderita

Figure 1. Ventral view of plates of 25 mm. nymph of Macromia caderita from Hays County.

Figure 2. Right ventral and dorsal plates of a 24 mm. Macromia caderita nymph from Uvalde County.

Figure 3. Right ventral and dorsal plate of a 22 mm. Macromia sp. (not M. caderita) nymph from Henderson County.

Scale: 2 cm. = 1 mm.



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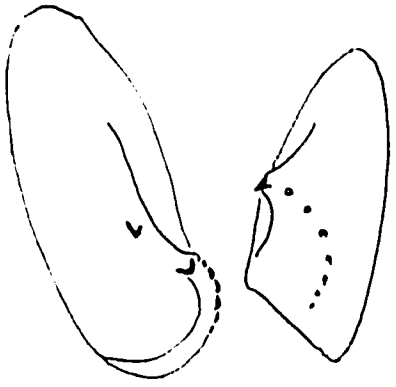

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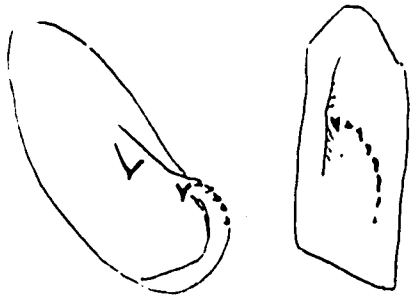

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PLATE XXIX

Didymops transversa

Figure 1. Ventral view of plates of a 26 mm. nymph.

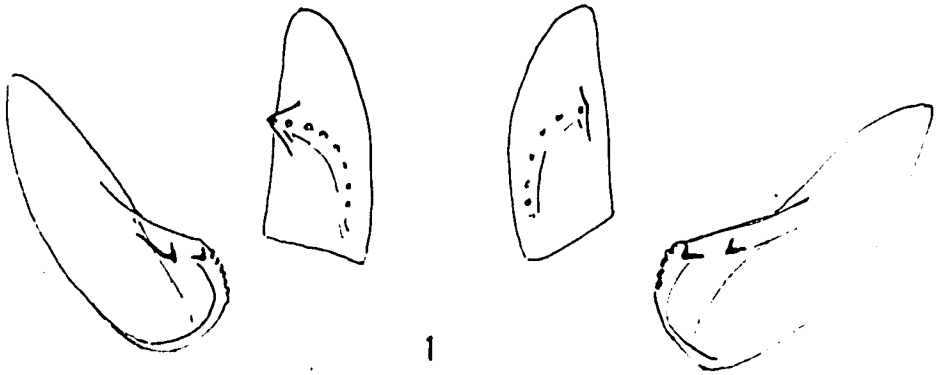
Scale: 2 cm. = 1 mm.

Figure 2. Three views of the right ventral plate of 11 mm. nymph showing the extra spine.

Scale: 2 cm. = 0.33 mm.

Figure 3. Enlargement of the left ventral plate of the figure one specimen to more clearly show the teeth on the lateral ridge.

Scale: 2 cm. = 0.33 mm.



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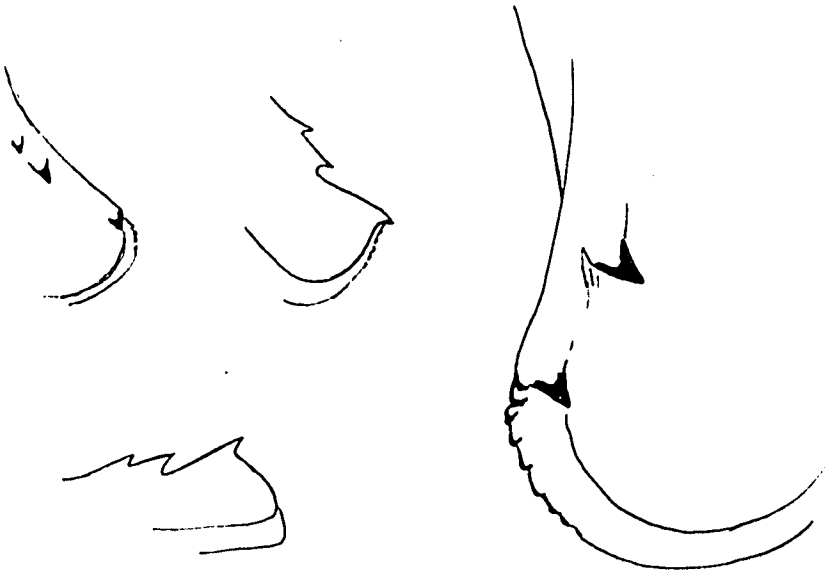

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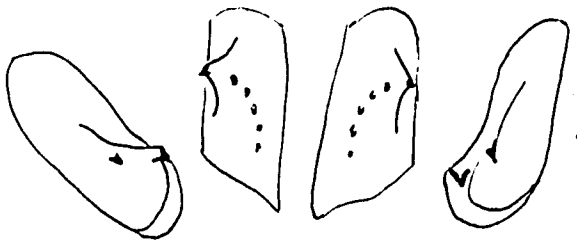
PLATE XXX

Tetragoneuria sp. and *Neurocordulia molesta*

Figure 1. Ventral view of plates of *Tetragoneuria* sp.

Figure 2. Ventral view of plates of *Neurocordulia molesta*.

Scale: 2 cm. = 1 mm.



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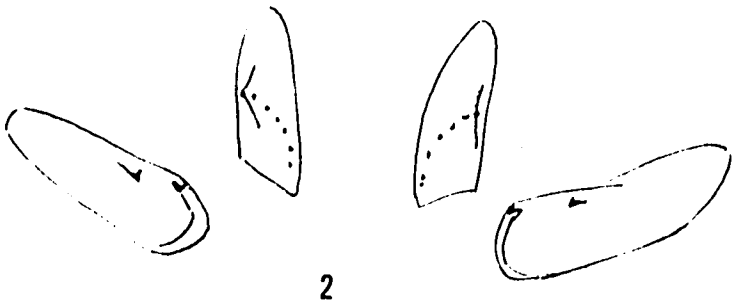

2

PLATE XXXI

Epicordulia princeps

Figure 1. Ventral view of plates.

Scale: 2 cm. = 1 mm.

Figure 2. Left dorsal plates, to show variation.

Figure 2. Median ridges of left dorsal plates of two specimens to show variation.

Figure 3. Terminal spines of the plates shown in figure 2, profile and lateral views.

Scale: 2 cm. = 0.33 mm.

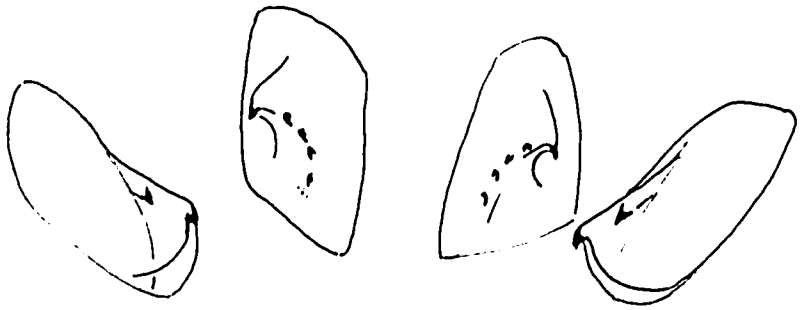

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PLATE XXXII

Epicordulia princeps

Median ridges of left dorsal plates of eight specimens to show variation.

Scale: 2 cm. = 0.33 mm.

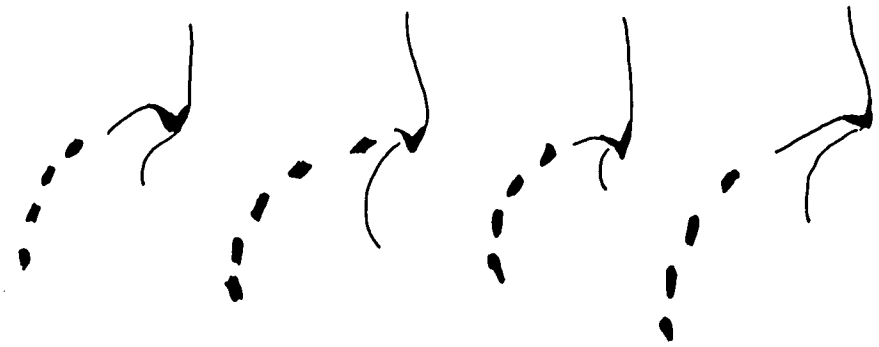


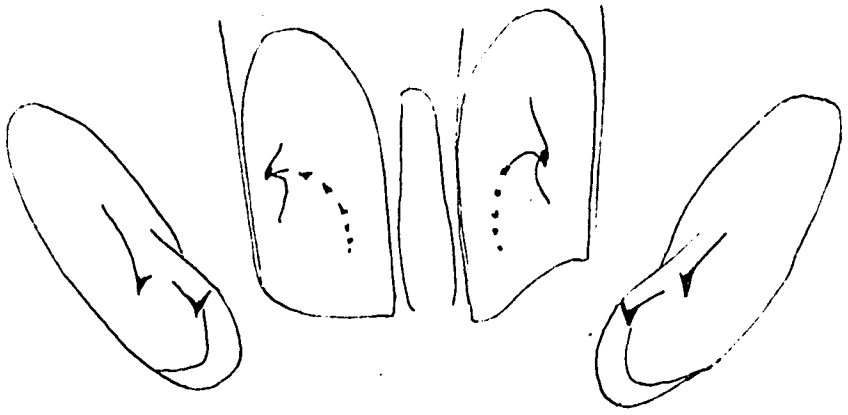
PLATE XXXIII

Somatochlora linearis

Figure 1. Ventral view of plates.

Figure 2. Proventriculus with muscle layers and epithelium removed to show arrangement of plates.

Scale: 2 cm. = 1 mm.



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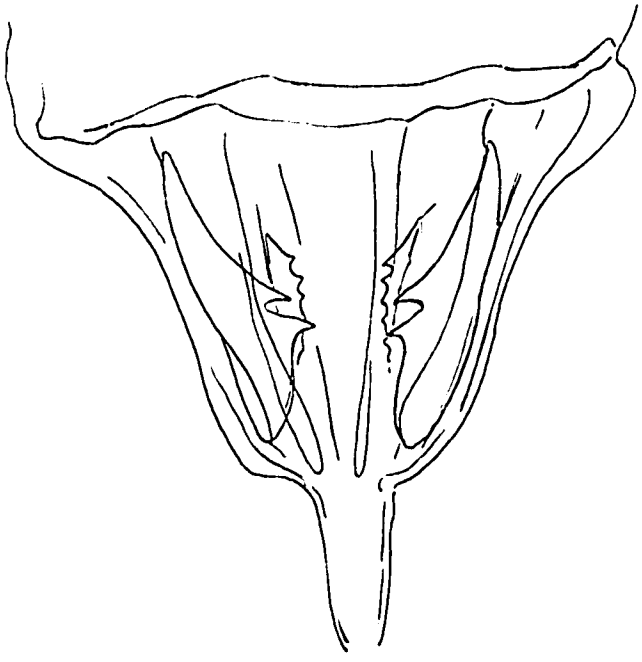


2

PLATE XXXIV

Erythemis simplicicollis

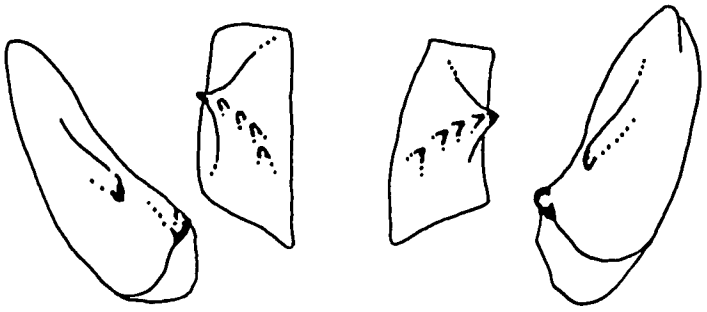
Figure 1. Ventral view of proventricular plates.

Scale: 2 cm. = 1 mm.

Figure 2. Ventral plates, lateral view.

Figure 3. Dorsal plates, lateral view.

Scale: 2 cm. = 0.33 mm.



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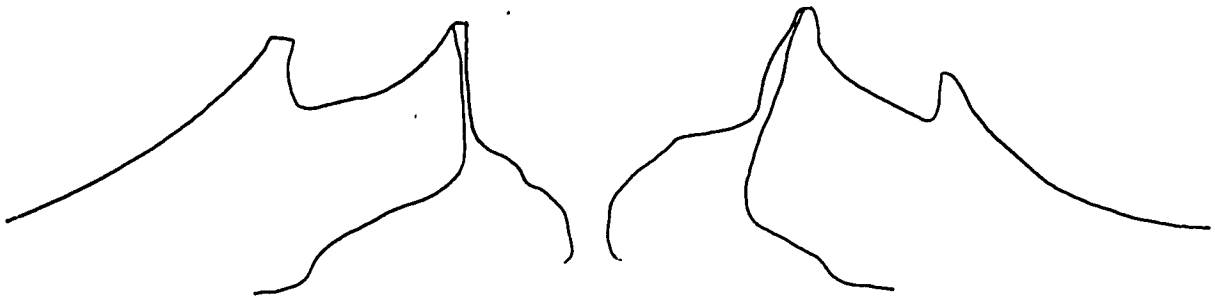

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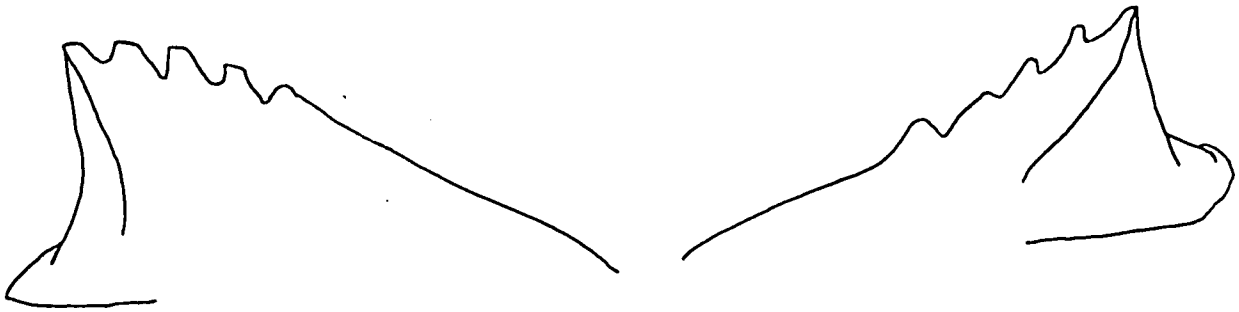

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PLATE XXXV

Erythemis simplicicollis

Figures to show variation.

Figure 1. Right ventral plate.

Figure 2. Right and left dorsal plates, profile view.

Figure 3. Right and left dorsal plates of specimen shown in figure 2.

1

2

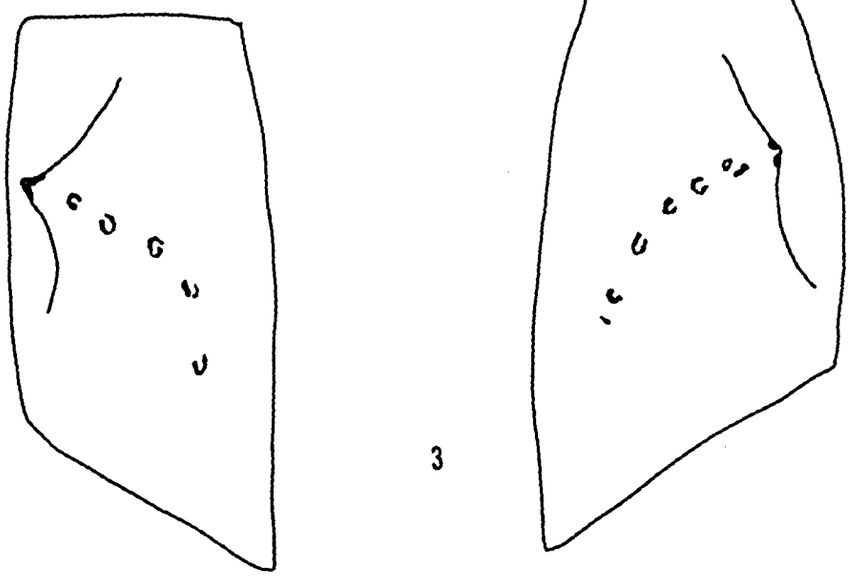

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PLATE XXXVI

Erythemis simplicicollis

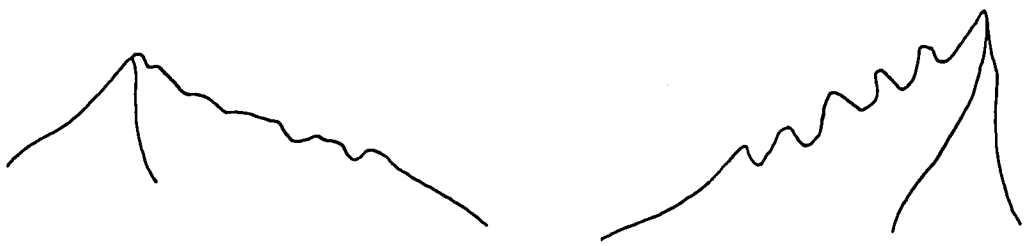
Figures to show variation.

Figure 1. Right and left dorsal plates of different specimens.

Figure 2. Right and left ventral plates of different specimens.

Figure 3. Right and left ventral plates of the same specimen.

Scale: 2 cm. = 0.33 mm.



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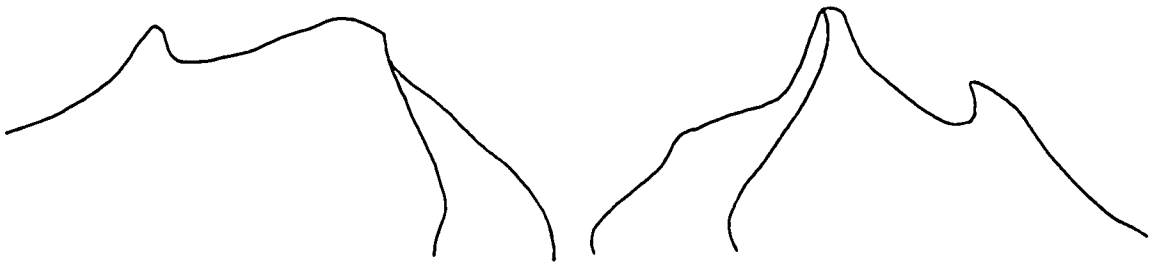

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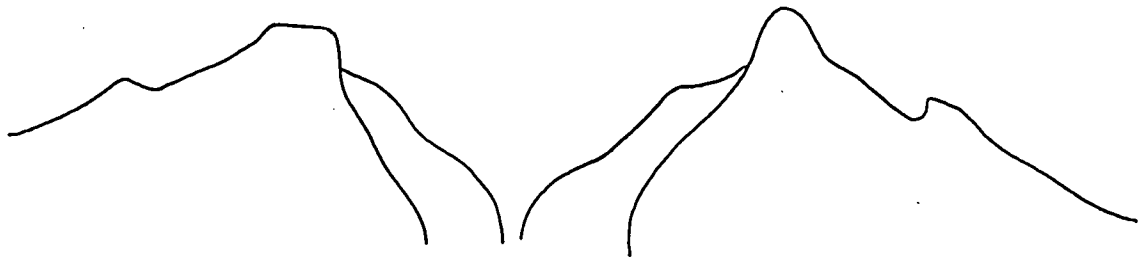

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PLATE XXXVII

Libellula auripennis

Figure 1. Ventral view of proventricular plates.

Scale: 2 cm. = 1 mm.

Figure 2. Right ventral plate and right dorsal plates, lateral view.

Scale: 2 cm. = 0.33 mm.

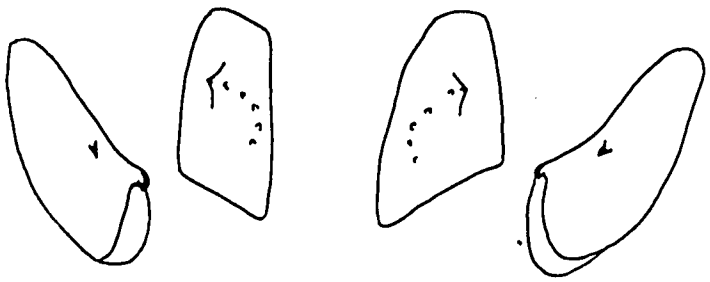

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PLATE XXXVIII

Plathemis lydia

Figure 1. Ventral view of proventricular plates.

Scale: 2 cm. = 1 mm.

Figure 2. Ventral plates, lateral view.

Figure 3. Dorsal plates, view showing the toothed ridges.

Scale: 2 cm. = 0.33 mm.

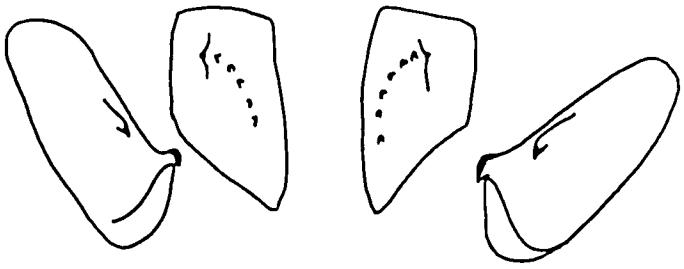

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PLATE XXXIX

Plathemis lydia

Figures to show variation.

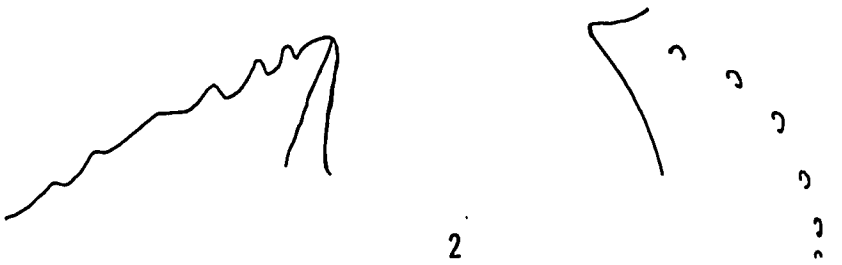
Figure 1. Left and right dorsal plates, two views, from the same specimen.

Figure 2. Left and right dorsal plates, two views, from the same specimen.

Figure 3. Right ventral plate and right dorsal plate of the same specimen.

Scale: 2 cm. = 0.33 mm.

1



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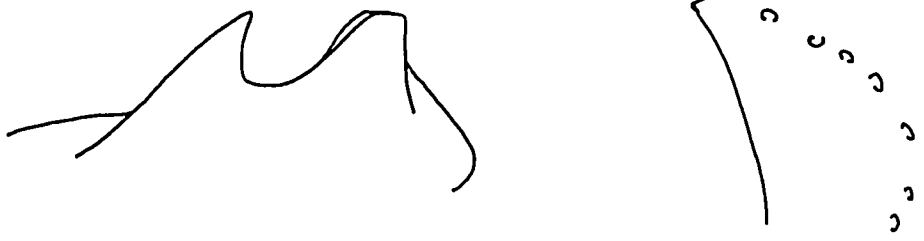


3

PLATE XL

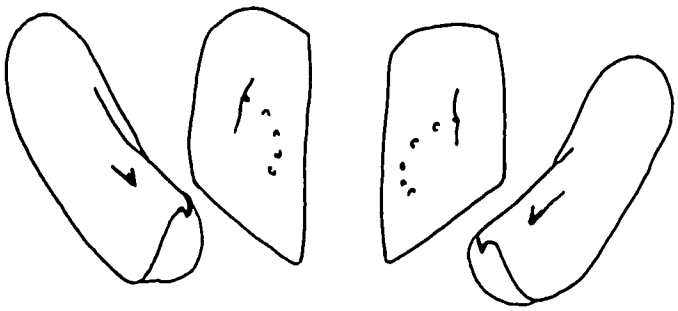
Orthemis ferruginea

Figure 1. Ventral view of proventricular plates.

Scale: 2 cm. = 1 mm.

Figure 2. Left dorsal proventricular plates of five specimens to show variation.

Scale: 2 cm. = 0.33 mm.



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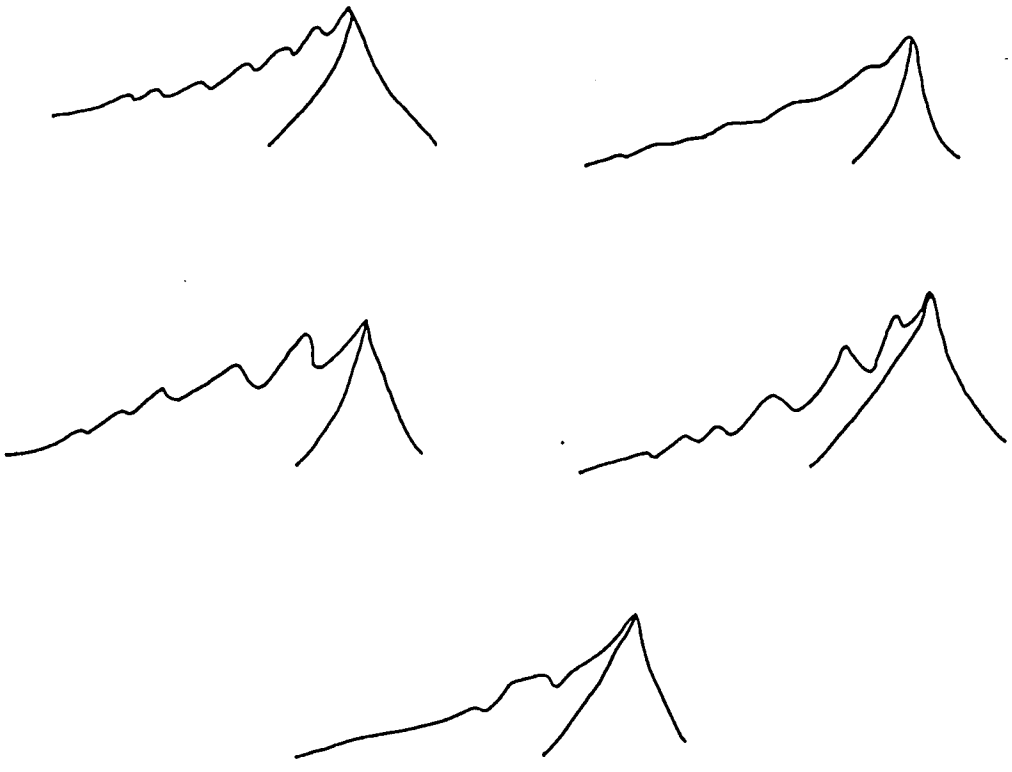

2

PLATE XLI

Pachydiplax longipennis

Figure 1. Ventral view of proventricular plates.

Scale: 2 cm. = 1 mm.

Figure 2. Left ventral plate, lateral view.

Figure 3. Dorsal plates, lateral view.

Scale: 2 cm. = 0.33 mm.

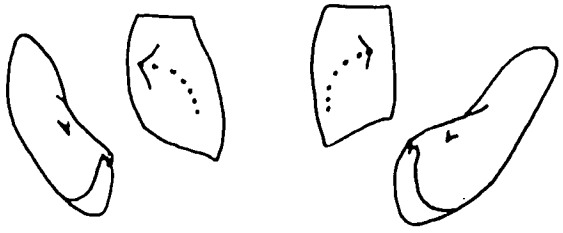

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PLATE XLII

Brechmorhoga mendax

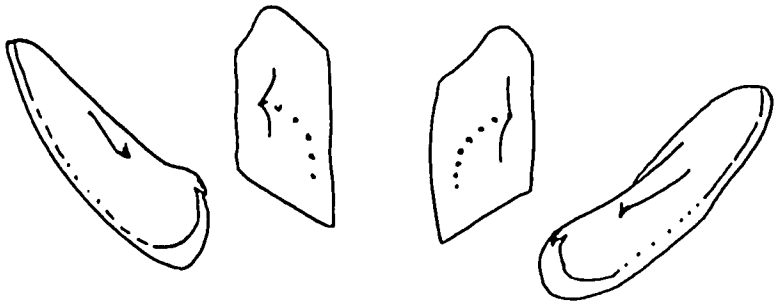
Figure 1. Ventral view of proventricular plates.

Scale: 2 cm. = 1 mm.

Figure 2. Right and left ventral plates, lateral view.

Figure 3. Right and left dorsal plates, lateral view.

Scale: 2 cm. = 0.33 mm.



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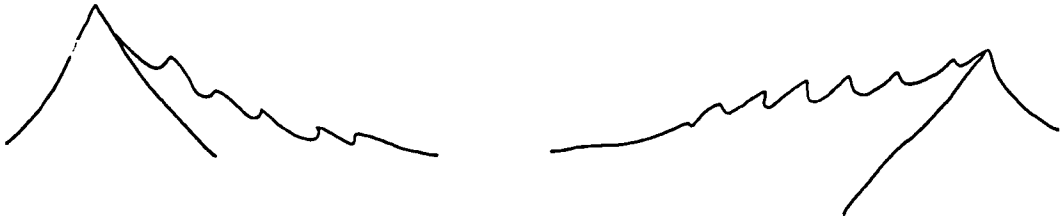

3

PLATE XLIII

Brechmorhoga mendax

Figures to show variation.

Figure 1. Dorsal plates of two different specimens.

Figure 2. Dorsal plates of two different specimens.

Figure 3. Ventral plates.

Scale: 2 cm. = 0.33 mm.

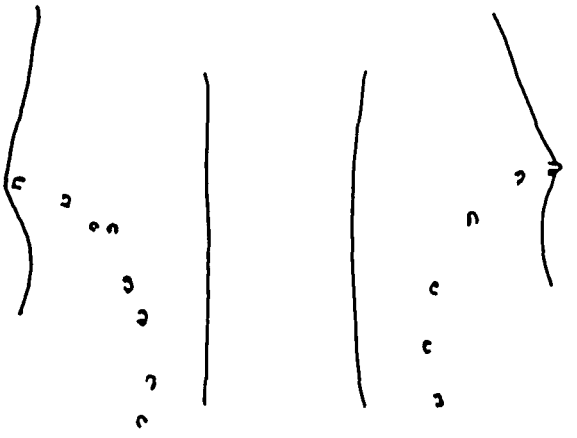

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PLATE XLIV

Perithemis tenera

Figure 1. Ventral view of proventricular plates.

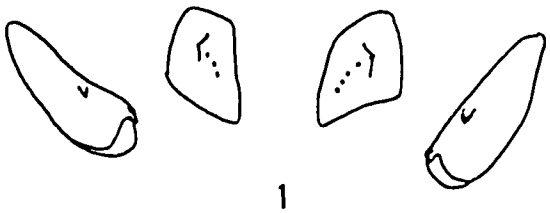
Scale: 2 cm. = 1 mm.

Figure 2. Left dorsal plate.

Figure 3. Dorsal plates, lateral view.

Figure 4. Left ventral plate.

Scale: 2 cm. = 0.33 mm.



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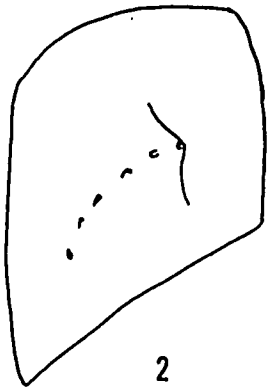

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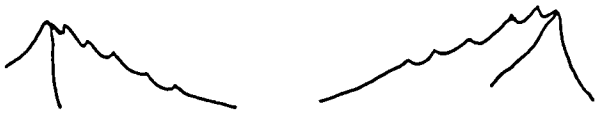

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4

PLATE XLV

Paltothemis lineatipes

Figure 1. Ventral view of proventricular plates.

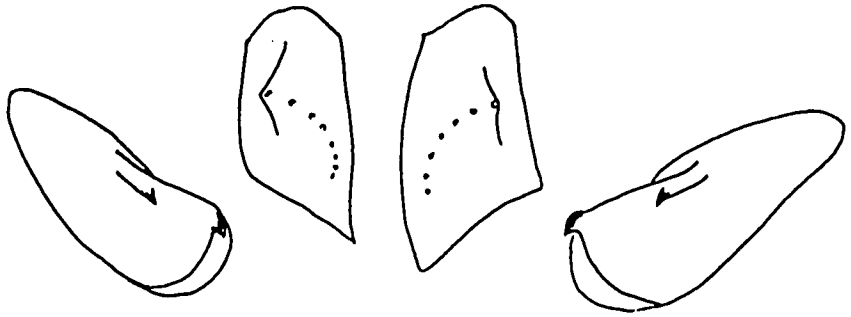
Scale: 2 cm. = 1 mm.

Figure 2. Right dorsal plate of a different specimen to show group of teeth at lower end of ridge.

Figure 3. Left dorsal plate of figure 1, lateral view.

Figure 4. Right ventral plate of specimen shown in figure 1.

Scale: 2 cm. = 0.33 mm.



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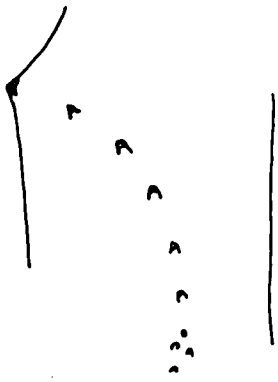

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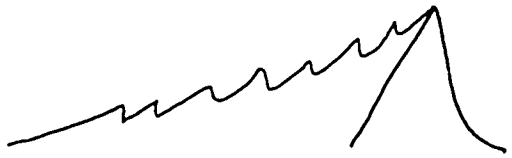

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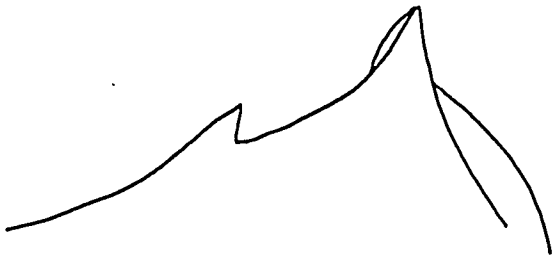


4

PLATE XLVI

Pantala hymenea

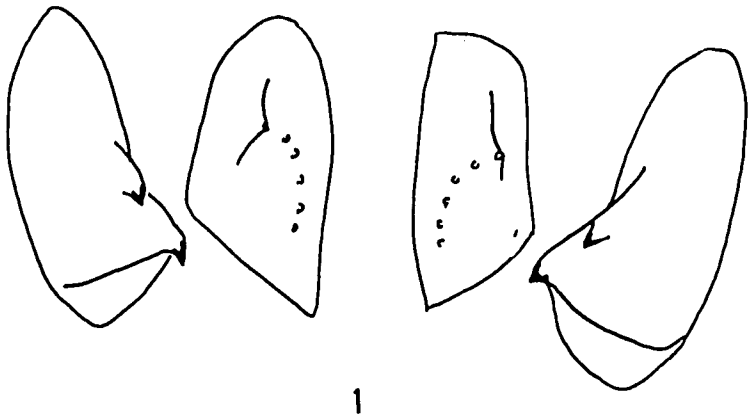
Figure 1. Ventral view of proventricular plates.

Scale: 2 cm. = 1 mm.

Figure 2. Ventral plates, lateral view.

Figure 3. Dorsal plates, lateral view.

Scale: 2 cm. = 0.33 mm.



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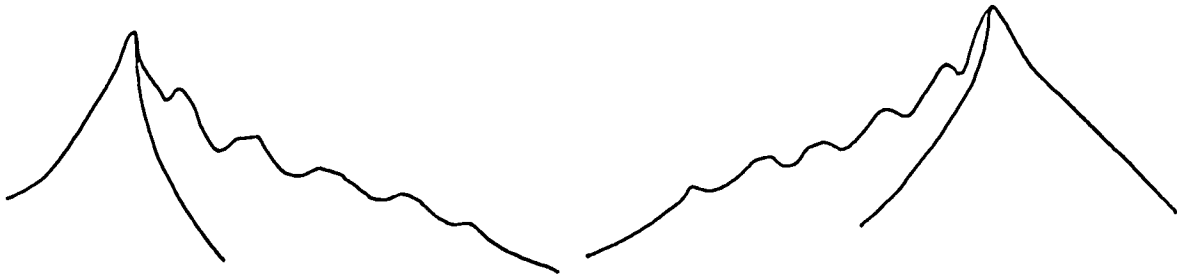


3

PLATE XLVII

Right ventral proventricular plates to show differences in size of spines.

Figure 1. Brechmorhoga mendax.

Figure 2. Perithemis tenera.

Figure 3. Paltothemis lineatipes.

Figure 4. Pantala hymenea.

Figure 5. Pachydiplax longipennis.

Figure 6. Erythemis simplicicollis.

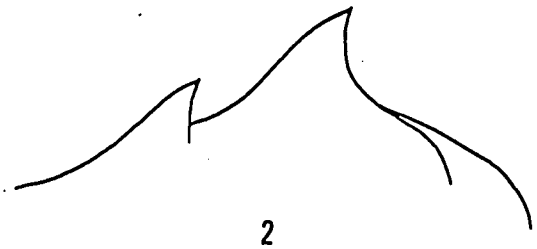
Figure 7. Orthemis ferruginea.

Figure 8. Plathemis lydia.

Figure 9. Libellula auripennis.

Scale: 2 cm. = 0.33 mm.

1



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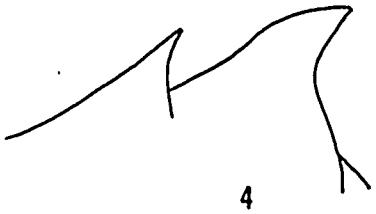

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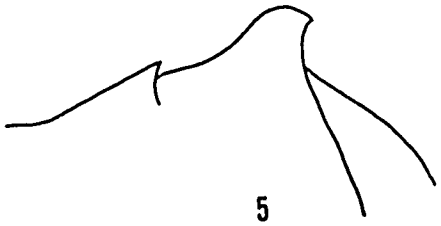

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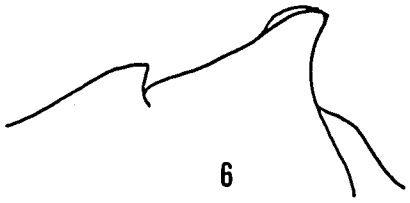

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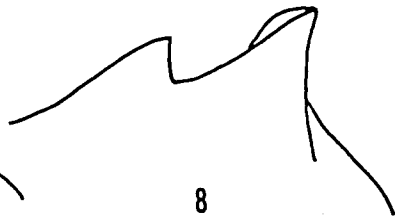

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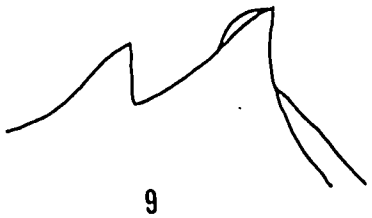

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PLATE XLVIII

Left ventral proventricular plates to show differences in direction in which the spines point.

Figure 1. *Libellula auripennis*.

Figure 2. *Pachydiplax longipennis*.

Figure 3. *Perithemis tenera*.

Figure 4. *Plathemis lydia*.

Figure 5. *Erythemis simplicicollis*.

Figure 6. *Paltothemis lineatipes*.

Figure 7. *Brechmorhoga mendax*.

Figure 8. *Orthemis ferruginea*.

Figure 9. *Pantala hymenea*.

Scale: 2 cm. = 0.33 mm.

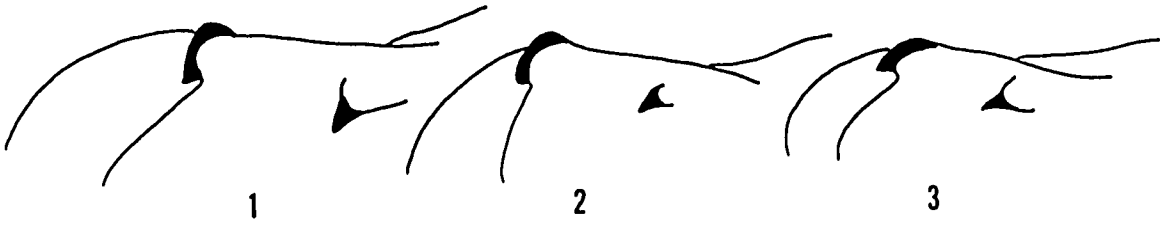
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PLATE XLIX

Profile view of lateral surfaces of the elevated areas of the left dorsal plates to show differences in the apex.

Figure 1. Perithemis tenera.

Figure 2. Erythemis simplicicollis.

Figure 3. Brechmorhoga mendax.

Figure 4. Pachydiplax longipennis.

Figure 5. Libellula auripennis.

Figure 6. Orthemis ferruginea.

Figure 7. Pantala hymenea.

Figure 8. Paltothemis lineatipes.

Figure 9. Plathemis lydia.

Scale: 2 cm. = 0.33 mm.

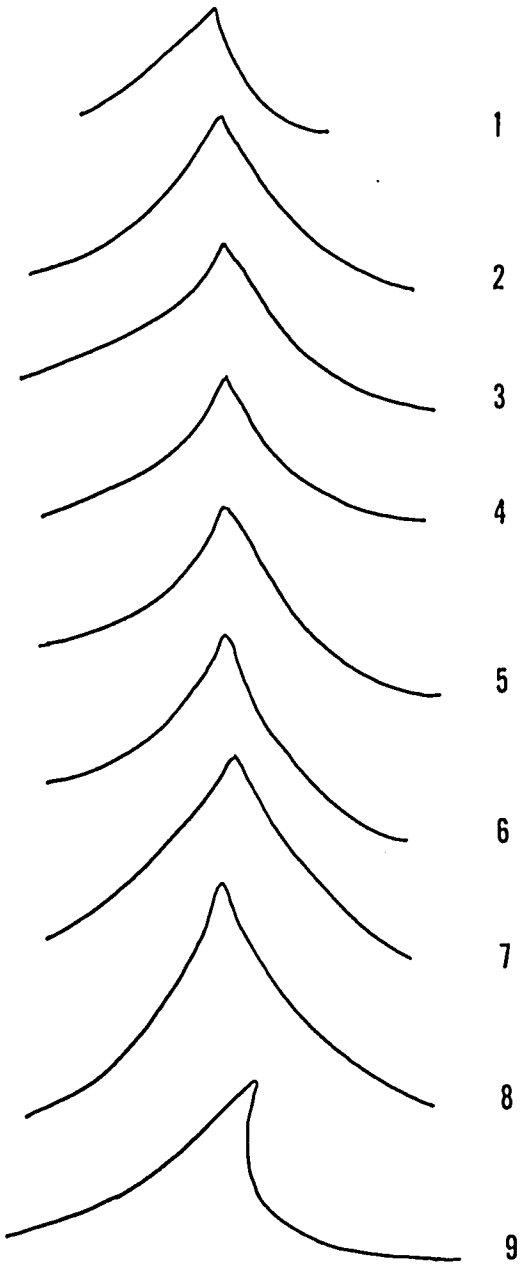
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PLATE L

Profile view of the terminal spines of the right ventral plates to show differences in the shape of these spines.

Figure 1. *Pachydiplax longipennis*.

Figure 2. *Libellula auripennis*.

Figure 3. *Plathemis lydia*.

Figure 4. *Orthemis ferruginea*.

Figure 5. *Erythemis simplicicollis*.

Figure 6. *Brechmorhoga mendax*.

Figure 7. *Pantala hymenea*.

Figure 8. *Perithemis tenera*.

Figure 9. *Paltothemis lineatipes*.

Scale: 2 cm. = 0.33 mm.

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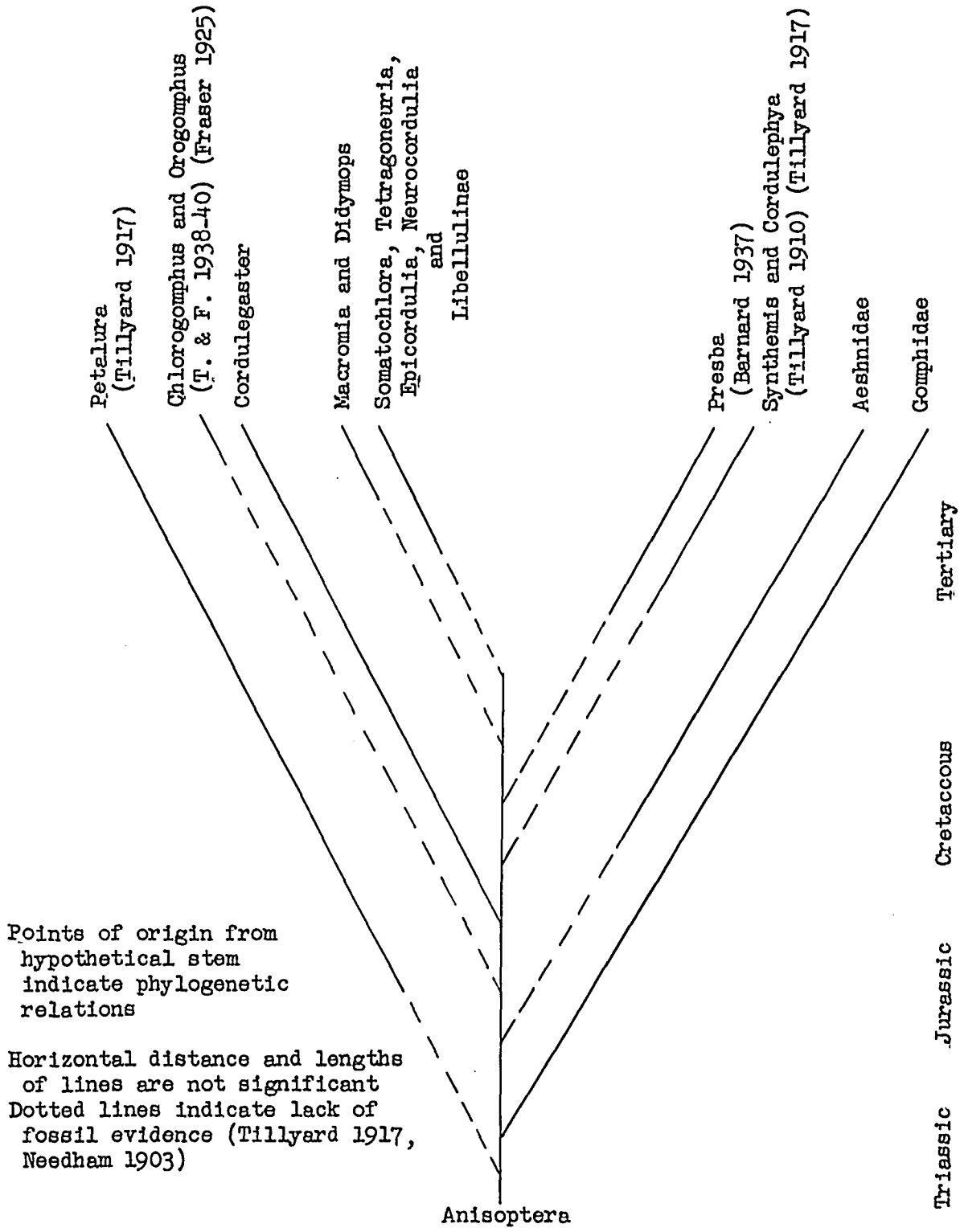

Figure 3. Phylogenetic relations of the major groups of Anisoptera

GENERAL PHYLOGENETIC CONSIDERATIONS

According to the structure of the proventricular armature, the divisions of the Anisoptera appear to be related in the manner as shown by the phylogenetic tree. The structure of the prototype of the Anisopteran proventriculus can be postulated only on the basis of the conditions existing in the primitive groups of present day Odonata. Since the Zygoptera (Ris 1896, Tillyard 1917) have eight to sixteen proventricular plates, and the Anisozygopteran, Epiophlebia laidlawi Tillyard, has eight plates, the primitive Anisozygopteran may also be assumed to have had eight plates. In this form the plates were probably long and scarcely differentiated from the folds anterior and posterior to them. The spines were numerous, small, scattered, and were pointed in a posterior direction.

Petalura gigantea Leach, of the archaic family Petaluridae, must have diverged from the main stem early in the evolution of the Anisoptera. According to Tillyard (1917), this Petaluran has eight very short proventricular plates with one to six small spines that point in a posterior direction. Although the primitive number of eight plates was retained, the tendencies of reduction in length and in spine number, which appear to different degrees in various extant Anisoptera, were manifest in this genus.

The Gomphid stem type probably emerged next. It differed from the primitive Anisopteran only in the reduction of the number of plates from eight to four. Early in the history of the Gomphids one branch

acquired additional spines (the minor reverse spines) in the posterior part of the proventriculus on the four plate-bearing folds. Two of the genera studied exhibit these spines. In Progomphus they appear to be fully developed in comparison with the spines of the typical plates, but in Aphylla they are reduced in size and even may be absent on some of the folds. I am postulating that these minor reverse spines are of secondary development rather than of ancient origin in the Gomphid stem type. I have observed them in only the two genera, one of which (Aphylla) is the most specialized of the Gomphidae studied. Since no anteriorly directed spines are present in any other Anisoptera observed or in any Zygoptera (according to the published figures I have checked), this appears to be a unique characteristic in the proventriculus of Aphylla and Progomphus.

The prototype of the Aeshnidae, no doubt, developed from a Gomphid-like stem form. The plates in the Aeshnidae have central raised areas with the highest point about two-thirds the distance from the anterior end. Most of the scattered spines were lost, the remaining ones are on the highest area. In Anax junius (Drury) lateral and median ridges are indicated by a reduction in size and concentration of the spines in those areas. Three lightly sclerotized intercalary folds are present between the plates in the Aeshnidae; thus, connecting this family with the primitive sixteen plate condition common in the Zygoptera.

After the divergence of the Aeshnidae, the stem form acquired a well developed pointed apex. The surface spines decreased in number, and clearly defined lateral and median toothed ridges were formed.

Chlorogomphus (Tillyard and Fraser 1938-1940) and Orogomphus (Fraser 1925) branched off early with an extreme development of the apices and with the loss of all the surface spines on one pair of plates

in Orogomphus.

In the Cordulegasterine branch all of the surface spines were lost, the apices became less pronounced, and there was an increase in the size of the lateral surfaces of the raised areas of the dorsal plates resulting in strong bilateral symmetry. A tendency toward the reduction in the teeth on the lateral ridges of the dorsal plates appears to be present in this genus.

The main stem form, after the divergence of the Chlorogomphines and Cordulegasterids, retained the toothed lateral and median ridges and lost most of the surface spines. The apical spine and one or two spines anterior to it remained. These spines increased in size.

Presba venator Barnard (Barnard 1937), Synthemis eustalacta (Burmeister) (Tillyard 1910), and Cordulephya pygmaea Selys (Tillyard 1917), according to my interpretation of the published figures, apparently branched from the original stem at this stage. Cordulephya and Synthemis have one pair of plates with two spines and without teeth on the lateral and median ridges. Presba, probably the most primitive of the three, retained the toothed lateral and median ridges and an additional spine in front of the anterior spine. This latter spine is interesting because a similar one was present in an eleven millimeter nymph of Didymops, a Macromiine in which this spine is normally absent.

The stem form now probably underwent a number of changes. The ventral plates lost the dentition on the median ridges. Their median surfaces increased in size with a corresponding decrease in the height of the lateral and in the width of the posterior surfaces. The lateral surface of the dorsal plates became smaller and the lateral ridges lost their teeth. At this point the Didymops - Macromia group originated.

The last major change in the stem form was the disappearance of

the dentition of the lateral ridges of the ventral plates. The Corduliinae genera that I have studied (Neurocordulia, Somatochlora, Epicordulia, and Tetragoneuria) and the Libellulinae have plates of this type. The only difference that appears to separate the above mentioned group from the Libellulinae is the relationship of the lateral and median ridges of the ventral plates of the first group. They are almost parallel while those of the Libellulinae are slightly more divergent.

The phylogenetic affinities of the divisions of the Anisoptera, based wholly on the structure of the proventriculus presented in the preceding paragraphs, differ in several aspects from the arrangement given by Tillyard and Fraser (1938-1940). These authors considered the Gomphidae more primitive than the Petaluridae, the Cordulegasteridae more primitive than Chlorogomphinae, and considered the Chlorogomphinae and both the Corduliinae and Libellulinae arising by common origin from the Cordulegasteridae. As shown by my diagram, I postulated the origin of the various groups from extinct stem forms that progressively developed as the precursors of our modern groups branched from them. The morphology of the proventricular armature of the Corduliinae (sensu Tillyard and Fraser 1938-1940) emphasizes the close relationship between this group and the Libellulidae (sensu Tillyard and Fraser).

The armature offers no evidence to support the separation of Neurocordulia from Tetragoneuria, Epicordulia, and Somatochlora as given by Williamson (1908). I agree with Needham (1908) in that these genera should be grouped together. Both Williamson (1908) and Needham (1908) place Synthemis in the group with Macromia and Didymops. According to my interpretation of the published figure of the armature of Snythemis

(Tillyard 1910), I believe it should be in a separate group as given by Tillyard and Fraser (1938-1940). I agree with Needham (1901) that the Macromiinae are worthy of subfamily rank. Barnard (1937) stated that Macromia picta Selys has armature similar to that of Presba as figured by Barnard (1937). The lateral and median ridges of both the dorsal and ventral plates in Presba have teeth, while they are absent from the lateral ridges of the dorsal plates and median ridges of the ventral plates of Macromia and Didymops. The apical spines of the ventral plates do not appear to be well developed in Presba, and the lateral surfaces of the elevated area of the dorsal plates in Presba are not reduced. The figure of Cordulephya (Tillyard 1917) appears to support the position of Tillyard and Fraser (1938-1940) who elevated this group to the rank of subfamily.

I realize that these data concerning the Corduliines are very incomplete, but the evidence seems to be of sufficient importance to serve as a basis for postulation. Although the Corduliidae and the Libellulidae (both families sensu Tillyard and Fraser) are united by the presence of the two spines on one pair of plates, the question arises as to whether this is of more significance than the resemblance of the other pair of plates of the aberrant Corduliines to the plates of Cordulegaster and the Chlorogomphinae.

I agree with Ris (1896) and Tillyard and Fraser (1938-1940) rather than with Needham (1951) in the relative position of the Cordulegasteridae.

As additional investigations are made concerning comparative morphology (both external and internal), serological affinities, chromosomal complements, ecological habits, and all correlated with

the past work on phylogeny, the solution of the interrelations of the groups of Odonata will be more nearly approximated.

KEY TO NYMPHS BASED ON THE PROVENTRICULAR ARMATURE *

1. Proventriculus with 8 armed plates....Petaluridae (Petalura gigantea)

   Proventriculus with four armed plates..... 2

2. Spines scattered over the entire (or almost entire sclerotized area, no toothed ridges present..... Gomphidae

   Spines limited in distribution..... 3

3. Plates alike; radial symmetry..... Aeshnidae

   Dorsal plates of contrasting structure from ventral plates; bilateral symmetry. (In the Chlorogomphinae the only difference between dorsal and ventral plates is the absence of spines on one pair)..... 4

4. Ventral plates with two large spines, an apical spine and one just anterior to it on the highest area of the plate. The anterior spine may have a secondary spine on its surface...Libellulidae

   Ventral plates without the second large spine directly anterior to the apex. There may be several scattered spines on the elevated surface, or all spines may be absent..... 5

5. One pair of plates with spines scattered over elevated surface, or with several spines near base at anterior end of elevated surface..... Chlorogomphinae

   Plates without spines on elevated surface or at basal anterior end of elevated area.....Cordulegasteridae

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*NOTE: This key includes the following species from the descriptions given in the literature: Anax papuensis, Anax imperator, Presba venator, Synthemis eustalacta, and Cordulephya pygmaea.

GOMPHIDAE

1. Plates narrow; dorsal plates of contrasting shape in profile view from ventral plates; minute minor reverse spines present (very difficult to see)..... *Aphylla williamsoni*

   All plates similar in general structure..... 2

2. Minor reverse spines present..... *Progomphus obscurus*

   No minor reverse spines present..... 3

3. Spines 27 or less in number, almost uniform in size (no very large spines)..... 4

   Spines 27 to 41 in number; spines on the high middle area are very large..... *Dromogomphus*

4. Length of plate five times width or less..... 5

   Length of plate equals six to ten times its width; spines 6 to 20 in number..... 6

5. Length of plate less than four times width; spines 7 to 10 in number..... *Hagenius brevistylus*

   Length of plate approximately five times width; spines 12 to 27 in number..... *Gomphoides*

6. Length of plate ten times width..... *Gomphus* (*Arigomphus*)

   Length of plate six times width..... 7

7. Length of plate seven or eight times width; spines 6 to 12 in number..... *Gomphus* (*Stylurus*)

   Length of plate six times width; spines 10 to 22..... 8

8. Posterior end of plate slightly higher than anterior end; spines 14 to 20 in number..... *Gomphus* (*Gomphus*) *exilis*

   Posterior end of plate not higher than anterior end..*Ophiogomphus*
   Erpetogomphus

AESHNIDAE

1. With 3 or more spines on raised areas..... 2

   With 2 spines laterally arranged at apex, no others present.....

   ..... *Anax papuensis*
   Anax imperator

2. Spines in one definite row from apex to base on either side..... 3

   Spines not in a definite row from apex to base on either side.... 4

3. Basal spines anterior to the apical spine..... *Boyeria vinosa*

   Basal spines posterior to the apical spine..... *Aeshna umbrosa*

4. Apical angle from side view approximately 50°; 6 to 9 spines..... 5

   Apical angle from side view 70° to 110°, usually 90° to 110°; spines 5 to 26..... 6

5. Spines 6 to 9 in number in somewhat of a rwo from apex to base on either side..... *Coryphaeschna ingens*
   Epiaeschna heros

   Spines 10 to 15 in number..... *Anax amazili*

6. Two or three apical spines larger than the other spines which are small and equal in size..... *Anax junius*

   Spines graduated in size or equal..... 7

7. With 6 or more spines on the surface posterior to the apex of the plate..... *Basiaeschna janata*

   With not more than 4 spines on the posterior surfaco; there may be several that form a row from the apex to the base on the lateral surfaces..... 8

8. Spines 10 to 13 in number, smaller in proportion to size of plate..... *Anax walzinghami*

   Spines usually fewer in number (5 - 12), larger in proportion to size of plates..... *Nasiaeschna pentacantha*

LIBELLULIDAE

1. Lateral and median ridges of both pairs of plates toothed; the anterior spine with a secondary spine on its surface..... ..... *Presba venator*

   Lateral and median ridges of both pairs of plates not toothed..... 2

2. With teeth on the lateral and median ridges of one pair of plates..... *Synthemis eustalacta* *Cordulephya pygmaea*

   On ventral plates teeth absent, or present on only the lateral ridges..... 3

3. Ventral plates with lateral ridges toothed..... Macromiinae

   Ventral plates without teeth on lateral and median ridges..... Corduliinae Libellulinae

CORDULIINAE AND LIBELLULINAE

Since there is such a great degree of similarity among the members of these two groups, I am not including a key for their identification.

SUMMARY

1. An investigation was made concerning the morphology of the proventriculus of immature Anisoptera with reference to its use in taxonomy.

a. The genera of the Gomphidae that can be easily recognized by the proventricular armature are the following: Progomphus, Gomphoides, Aphylla, Hagenius, Dromogomphus. The genera Erpetogomphus, Ophiogomphus, Gomphus (Arigomphus), Gomphus (Stylurus), Gomphus (Gomphus) show some differences in their armature, but this study does not indicate the proventricular plates to be very useful in distinguishing these genera. On the species level, Dromogomphus spoliatus and Dromogomphus spinosus can be distinguished by their armature.

b. Of the Aeshnidae Boyeria, Aeshna, Basiaeschna can be characterized by the structure of their proventricular plates. Epiaeschna and Coryphaeschna have plates that are almost similar but may be separated from the other genera studied. Nasiaeschna differs in the structure of the armature but the differences are not sufficient to permit ease in identification. Anax junius and Anax amazili may be distinguished both from each other and from the other Aeshnidae studied. Anax walzinghami is intermediate between Anax junius and Anax amazili, but can be separated from the others. There is greater diversity among the species of Anax than among the several other genera of Aeshnidae studied.

c. The genera Didymops and Macromia of the Macromiinae cannot be distinguished from each other by the structure of their armature. The

Macromiinae, however, are unique from the other Libellulidae studied.

d. The proventricular plates of the genera of Corduliinae and Libellulinae are much alike; thus, are not useful in taxonomy.

e. The number of both spines and teeth varies among individuals of a species; therefore, this characteristic is useful to a very limited degree in taxonomy.

2. The phylogenetic relations based entirely on the structure of the armature of the genera of Gomphidae, Aeshnidae, and Libellulinae are discussed. The most important results indicated are the following:

a. The direct relationship between Progomphus and Aphylla is corroborated by the presence of the minor reverse spines, a characteristic unique in these two genera. Gomphus (Arigomphus) appears to be the most primitive subgenus of the genus Gomphus and is one of the more primitive Gomphines. That bilateral symmetry is evidenced in the structure of Aphylla, as well as in some of the higher families, indicates that this is a fortuitous evolutionary trend, having appeared more than one time in the suborder.

b. This study substantiates the view that Basiaeschna is a primitive Aeshnine and that Anax is a highly specialized genus of this family. It does not corroborate the origin of Coryphaeschna from Aeshna and the wide seperation of Aeshna and Boyeria.

c. The structure of the proventricular plates supports the arrangement of the genera of the Libellulinae.

3. The phylogenetic relations of the major groups of the Anisoptera are given. The Petaluridae are considered as being derived from a primitive Anisopteran stem form with eight proventricular plates. The Cordulegasteridae are considered more advanced phylogenetically than

the Chlorogomphines. The higher Corduliines resemble the Libellulinae.

4. No sexual dimorphism in the structure of the proventricular armature was observed.

5. The ontogenetic development of the proventriculus of the nymph was studied. There is no correlation between the number of spines and the size of the nymph.

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